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BIOSYSTEMATIC STUDY OF CHAMAESARACHA (SOLANACEAE)[1]

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Chamaesaracha was established as a genus by A. Gray in 1876, having previously been recognized as a section of *Saracha*. The genus has been treated in part by Gray (1878) and by Rydberg (1896). However, an inclusive revision of *Chamaesaracha* has not been forthcoming.

As herein conceived, *Chamaesaracha* is an exclusively North American genus with its greatest concentration of species in the Chihuahuan desert. A total of 18 species has been attributed to the genus, but only 7 are recognized in the present treatment. The remaining 11 have been relegated to synonymy or have been transferred to other genera (see excluded species).

CHROMOSOME STUDIES

Meiotic chromosomes were observed best at anaphase I, because of clumping and poor staining of the chromosomes in diakinesis and metaphase I. The latter is particularly notable in polyploid cells. Except for several triploid individuals, meiosis appeared to be regular with equal separation of chromosomes at anaphase I. All chromosome numbers reported here are from meiotic material.

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Several of the earlier chromosome number reports for *Chamaesaracha* (Powell and Averett, 1967) require clarification in keeping with the results of my present systematic account of the genus. In the 1967 paper, counts were listed for the following: *C. coronopus* (*n* = 24); and *C. cf. sordida* (*n* = 12, 18, 36). With the exception of *C. sordida* and *C. cf. sordida*, all of the 1967 reports were applied to taxa that were correctly identified. (*C. cf. crenata* is *C. crenata*). The following corrections must be noted in regard to the 1967 reports attributed to *C. sordida* and *C. cf. sordida*: The *n* = 12 and *n* = 18 collections identified as *C. cf. sordida* are now recognized as *C. sordida*. The *n* = 24 populations referred to *C. sordida* are now regarded as *C. coniodes*, a species then regarded as conspecific with *C. sordida*. *Chamaesaracha cf. sordida* (*n* = 36), except for *Averett* 155, is now recognized as *C. coronopus*. Collection 155 is *C. pallida*, a newly described taxon (Averett, 1971). Listed in Table 1 are additional counts for the taxa first reported in 1967, as well as reports for the remaining species of *Chamaesaracha*.

Polyploidy is found in five of the seven species of *Chamaesaracha*, four being typically polyploid. Although there are areas lacking convincing data some comment may be made regarding the origin of selected polyploids. Because each is somewhat unique, they are considered individually in the following discussion.

Chamaesaracha sordida. There is evidence for an autopolyploid origin of the triploid (*n* = 18) individuals in *C. sordida*. In a regional study of the taxon, a triploid plant was collected from a population in northern Culberson County, Texas. Meiosis in this individual was irregular. Diakinetic and metaphase chromosomes were not clearly observed, but unequal segregation of 36 chromosomes could be observed in anaphase I. From 14 to 22 chromosomes could be found going to one side of the diad in about 100 cells, but 18 choromsomes could be observed in one side or the other of an equivalent number of cells. The irregularity was first attributed to hybridization between a diploid and a tetraploid. However, subsequent resampling of the area from which the triploid individual was collected indicated that only diploid individuals occurred in the population concerned. (Chromosome numbers were ascertained for about 15 individuals from the general area; all were diploid with $n = 12$).

Two additional triploid individuals have been found in widely disjunct populations of the same species. These have not been carefully studied, but in one population in Yoakum County, Texas, chromosome numbers from three individuals were determined (*Averett* & *Tomb* 320A, B, C). One of these was triploid and the other two were diploid. The only other triploid found in this species came from a population in Lincoln County, New Mexico.

The morphology and flavonoid chemistry of the triploids referred to above are nearly identical to that of the diploids. Considering the sporadic occurrence of the triploids, the plants do not seem to have a common origin nor do they appear to be the result of the interspecific hybridization. Rather, each appears to have had an independent origin through the chance fertilization of an unreduced gamete with a normal haploid gamete. The additional set of chromosomes would account for the observed unequal chromosomal segregation found in the triploid populations.

Chamaesaracha coronopus. This species is typically tetraploid with $n = 24$, but occasional diploids ($n = 12$) and hexaploids ($n = 36$) are found in western and southwestern Texas and also in southeastern Arizona. Unlike the triploids of *C. sordida,* the hexaploids are quite fertile. Meiosis appears to be regular, at least in anaphase I, and unequal segregation has not been observed. Additionally, seed set and germination is approximately equivalent to that of the tetraploids. Because of their apparent fertility, an autoploid origin such as proposed in *C. sordida* does not seem likely. However, as in the triploid *C. sordida,* there is no evidence that another taxon has contributed to the genome of the hexaploids in question, even though *C. sordida* ($n = 12$) does occur sympatrically in some areas with *C. coronopus*. Rather, the hexaploids concerned appear to be derived from hybridization between the diploid and tetraploid races of *C. coronopus*. Chemical and morphological data are currently being accumulated and preliminary results appear to confirm this suggestion.

Evidence is not available to suggest the origin of the tetraploid race of *C. coronopus* and the remaining polyploid species of *Chamaesaracha*. However, two species, *C. pallida* ($n = 36$) and *C. edwardsiana* ($n = 24$) are believed to be closely related to, and derived from, *C. coronopus* or its ancestors. *Chamaesaracha coniodes* is not particularly close to any of the former species and is likely independently derived. Autoploidy or segmental alloploidy may account for the polyploidy in both *C. coniodes* and *C. coronopus* $n = 24$.

Table I. Chromosome numbers and number of plants counted of *Chamaesaracha*.[3]

Taxon	Chromosome number (n)	Number of plants counted
C. coronopus[4]	12	3
C. coronopus	24	26
C. coronopus	36	5
C. coniodes	24	68
C. crenata	12	8
C. edwardsiana	24	11
C. pallida	36	6
C. sordida	12	53
C. sordida	18	3
C. villosa	12	8

[3] Data from Powell & Averett (1967) and Averett (1970).

[4] Not previously reported. Discussion & localities in text.

FLAVONOID STUDIES

Populations were sampled for flavonoid studies so as to represent as much of the total range, as well as intraspecific variability, of each of the species as time and opportunity permitted. One to ten individuals from the various populations were analyzed to determine the extent and significance of inter- and intrapopulational variation. Voucher specimens for the populations studied are deposited in the Herbarium of the University of Texas at Austin. Duplicate specimens will be distribued at a later date.

Flavonoids were extracted overnight from leaf material with 85% methanol and separated by two-dimensional paper chromatography. Solvent systems of t-butanol, glacial acetic acid, and water (3:1:1 v/v) and 15% glacial acetic acid were employed. The compounds detected were then characterized structurally by ultraviolet spectroscopy and appropriate acid and enzyme hydrolyses. The techniques utilized for chromatographic and spectral analysis follow those presented by Mabry, Markham and Thomas (1971).

All of the compounds extracted from *Chamaesaracha* are based on either quercetin or kaempferol skeletons. Differences among the several compounds primarily reflect glycosidic substitutions, but a few methoxylated compounds also are present. Except for the methoxylated compounds, the flavonoids of *Chamaesaracha* are the same as those reported for *Leucophysalis* by Averett and Mabry (1971), but greater interspecific variability is found in *Chamaesaracha.*

Flavonoid data, in general, were found to substantiate conclusions based upon morphological data. Two-dimensional chromatographic patterns were, for the most part, species-specific, showing relatively little variation, either within or between populations of the same species. A notable exception was found in *Chamaesaracha coniodes* in which significant variations in the flavonoid patterns were observed. This species is also quite variable morphologically and much of the flavonoid variation probably reflects genetic heterogeneity from population to population. Within the more discrete populations, however, flavonoid patterns were essentially uniform (this is also true of morphological variation).

Closely related taxa were found to have similar flavonoids; consequently, chemical data have been utilized for many of the taxonomic conclusions reached in the present study, especially in situations where morphological and chromosomal distinctions were not decisive.

BIOECOLOGY

Chamaesaracha, a closely knit genus of perennial herbs, is largely restricted to the desert regions of the southwestern United States and northern Mexico. The plants are fairly common along roadsides in early and later summer, but populations become depauperate in the hot, dry, midsummer period, being found with some difficulty, except in areas of accumulated moisture.

The plants often occur in closely clustered populations of 25-30 plants. Such populations likely originated from one or a few seeds, and are believed to be largely the result of vegetative reproduction from spreading rhizomes. In garden plots, individual plants form colonies 8-10 feet in diameter within a single growing season. Intrapopulational variation, both chemical and morphological, within these clusters is essentially absent, suggesting a single source for most of the individuals within a given population. Vegetative reproduction, along with perenniality of the rootstocks, must have much to do with the variation patterns, or lack of them, in the natural populations.

The role of vegetative reproduction and perennial habit becomes even more apparent when seed germination is considered. Although seed set is more than adequate, the percentage of seed germination is very low. In germination experiments, seeds were allowed to imbibe for about seven days. After imbibition, various exposures to light and dark were given, but the latter seemed to have little effect on germination. Typically fewer than 5% of the seeds germinated. Germination in diploid species was considerably lower than in polyploid species. It is presumed that seed germination is equally poor in nature, though this may not be a valid assumption.

Since fruit with relatively high seed set are found in nature, the various insects that visit the flowers must be fairly effective pollinators. No consistent pollen vectors have been observed, but bee flies and several types of small beetles are commonly found on the flowers of *Chamaesaracha*. Evidence for self-sterility has not been obtained for any of the species, but in isolated plants in garden plots, fruit was observed only on *C. crenata*. Even in this species, however, seed set was reduced some 80% from that found in nature. In the field, probably both self and out pollination occur, with outcrossing predominating.

GENERIC RELATIONSHIPS

Chamaesaracha is included in the tribe Solaneae (Wettstein, 1895) and has generally been associated with *Physalis* and *Leucophysalis*, largely because of their similar corolla forms. It is probably most closely related to *Leucophysalis*, differing in characters of the berry; whereas *Physalis* is separated primarily by its inflated fruiting calyx, and to some extent by its flower. The Asian genus *Physaliastrum* is related to *Chamaesaracha* in much the same way that the latter is related to *Leucophysalis*. *Physaliastrum* is, however, believed to be more closely related to *Leucophysalis;* indeed, they may well be congenic (Averett, 1971). All of the species that now comprise *Leucophysalis* and *Physaliastrum* have, at one time or another, been relegated to *Chamaesaracha*. In fact, workers are not generally in accord as to the preferred treatment of these several genera of Solaneae. For example, Waterfall (1958) suggested that *Physalis* and *Chamaesaracha* might be combined and treated as subgeneric categories. If these were the only two genera involved, the merger would not be unreasonable. However, under such a treatment, the status of *Margaranthus* would be affected since it is hardly more distinct from *Physalis* than is *Chamaesaracha*, differing only in the color and urceolate form of its corolla. While the sinking of *Margaranthus* with *Physalis* may also be reasonable, it is difficult, at least for me, to accept the merger of *Chamaesaracha* and *Margaranthus*. Other genera are interrelated in a similar manner, and for that reason it seems worthwhile to consider them in more detail.

Leucophysalis was established as a monotypic genus by Rydberg (1896) to accommodate *L. grandiflora,* formerly included in *Physalis* by Hooker (1928). Fernald (1949) compared *L. grandiflora* with certain Asian species of what he considered to be *Chamaesaracha,* and as a consequence transferred *L. grandiflora* to the latter genus. However, I have recognized *Leucophysalis* as distinct from *Chamaesaracha,* and have added an additional two species (Averett, 1971). The distinctive morphological features of the two taxa are comparable to those that differentiate most of the other genera of the Solaneae. *Leucophysalis* is similar to *Chamaesaracha* with respect to characters of the flower and the fruiting calyx, but differs in having a fleshy berry with a placenta extending the entire length of the berry. In *Chamaesaracha* the berry is dry, and the placenta is mostly basal (not extending the entire length of the berry). The species of *Chamaesaracha* are extremely uniform in floral, fruit, and seed morphology and as such, departure of the fruiting character seems significant. In addition, the two taxa have quite distinct habitat preferences and occupy different geographical regions. In contrast to the arid desert habitat of *Chamaesaracha, Leucophysalis* is found in more mesic habitats, e.g., the Sierra Nevada of California and the Great Lakes Region.

Physaliastrum is a small Asian genus of two species distinguished from *Leucophysalis* by the form of its corolla lobes, which are not plicate (as they are in *Leucophysalis*). The berry is like that of *Leucophysalis,* further differentiating the genus from *Chamaesaracha.*

Physalis differs from *Chamaesaracha,* as well as from *Leucophysalis* and *Physaliastrum,* in having a ribbed, inflated fruiting calyx. The only genus with a structure of this type is *Margaranthus,* which, as mentioned above, differs from *Physalis* in corolla shape. *Physalis* may be differentiated from *Chamaesaracha,* at least to some extent, on characters of the perianth. The corolla of *Physalis* is campanulate, and the flowering calyx is truncate. However, the floral morphology of *Chamaesaracha* is at least approached in a few species of *Physalis* (e.g., *P. lobata* and *P. wrightii*). *Physalis* is probably more closely related to *Margaranthus* on the basis of the fruiting calyx, and on other characters it is more closely related to *Leucophysalis* and *Physaliastrum* than it is to *Chamaesaracha.*

Nicandra is native of Peru, but is widly naturalized in the United States being found in wastelands and around old gardens. *Nicandra* is closely related to and often mistaken for *Physalis,* but differs in having 5 carpels and distinct, sagittate sepals.

Saracha is primarily a tropical genus of about 30 species extending from Peru through Central America north into northern Mexico and the southwestern United States.* *Chamaesaracha* and *Saracha* were once considered congeneric, but the two genera may be distinguished on fruiting characters. In *Saracha* the fruiting calyx is rotate and expanding at the base of a fleshy berry; in *Chamaesaracha* the fruiting calyx is tightly investing a dry berry. *Saracha* is probably not as closely related to *Chamaesaracha* as the genera mentioned above.

Oryctes is a monotypic genus of western Nevada and southeastern California, resembling *Chamaesaracha* in habit and somewhat in fruit. It is, however, easily distinguished by its small tubular flower and flat, orbicular seeds.

The few remaining genera of the Solaneae are not considered here since they are not so closely related to, and rarely confused with, *Chamaesaracha.*

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*Recent studies by W. G. D'Arcy and Johnny Gentry indicate that the Mexican and Central American species are properly treated as *Bellinia* R. & S. Earlier suggestions of affinity between *Saracha* and *Chamaesaracha* were likely based upon these species.

KEY TO CHAMAESARACHA AND RELATED GENERA

Flowers tubular, seeds orbicular . . . . *Oryctes*

Flowers campanulate to repand-rotate or urceolate, seed reniform,

  Fruiting calyx expanding under and not enclosing the berry . . . . *Saracha*

  Fruiting calyx loosely or tightly investing the berry . . .

    Calyx inflated around the berry.

      Flowers urceolate . . . . *Margaranthus*

      Flowers campanulate to repand-rotate.

        2 carpelate, calyx of united sepals . . . . . . *Physalis*

        5 carpelate, calyx of distinct, sagittate-based sepals . . . . *Nicandra*

    Calyx tightly investing the berry.

      Berry dry, placentation mostly basal, seeds rugose-reticulate . . . . *Chamaesaracha*

      Berry fleshy, placentation axile, seeds punctate.

        Flowers repand-rotate . . . . *Leucophysalis*

        Flowers campanulate . . . . *Physaliastrum*

PHYLOGENETIC CONSIDERATIONS

Chamaesaracha is largely restricted to the arid regions of the southwestern United States and northern Mexico. What are believed to be the more primitive, diploid species, *C. villosa, C. crenata* and *C. sordida,* have their centers of distribution in the Chihuahuan desert of northern Mexico. Of these, *C. sordida* is the only species to have any appreciable distribution in the United States. Still, it has a distinctly southern distribution as compared to the polyploid species, *C. coronopus* and *C. coniodes. Chamaesaracha coronopus* is the most widespread species, extending essentially over the entire range of the genus; *C. coniodes* is also widespread, but does not extend so far west as *C. coronopus.* The remaining polyploid species are fairly restricted in distribution, with *C. edwardsiana* occurring primarily on the Edwards Plateau of south-central Texas and adjacent Mexico and *C. pallida* extending from the Edwards Plateau into western Texas and northern Mexico.

From the distributional data, it seems reasonable to suggest that *Chamaesaracha* had its origin in the highlands of northern Mexico, the ancestral species of which probably belonged to the more xeric members of the Madro-Tertiary Geoflora (cf. Axelrod, 1958). With continued adaptation to xeric conditions, expansion from this area was likely concurrent with the spread of an arid environment to the north and east. In that the polyploid and derived species are marginal to the Chihuahuan desert proper, it is difficult to imagine an opposing direction of migration and speciation.

The interpretation of evolutionary trends in *Chamaesaracha* is based for the most part on chromosomal and distributional data in combination with correlated morphological features. Some of the characters that I consider to be primitive and derived, at least within *Chamaesaracha*, are listed below:

Primitive	*Derived*
1. woody rootstock	subligneous root
2. large, ovate, entire, and thin leaves	small, lanceolate, lobed, and thickened or leathery leaves
3. large flowers	small flowers
4. O-methylation of flavonoids	absence of O-methylation of flavonoids
5. increased glycosylation of flavonoids	decreased glycosylation of flavoids

The assessment of morphological characters generally follows classical consideration for those features (i.e., perenniality is generally considered primitive, as are large flowers). Polyploidy is considered to be derived in *Chamaesaracha*, quite apart from numerical considerations, because the polyploids possess fewer of the characters considered primitive in the listing above. Hence, the fairly widesperad occurrence of polyploidy offers a sound basis upon which to establish evolutionary trends within the genus.

Considering the above, it is possible to construct a schematic representation of the proposed origin and evolution

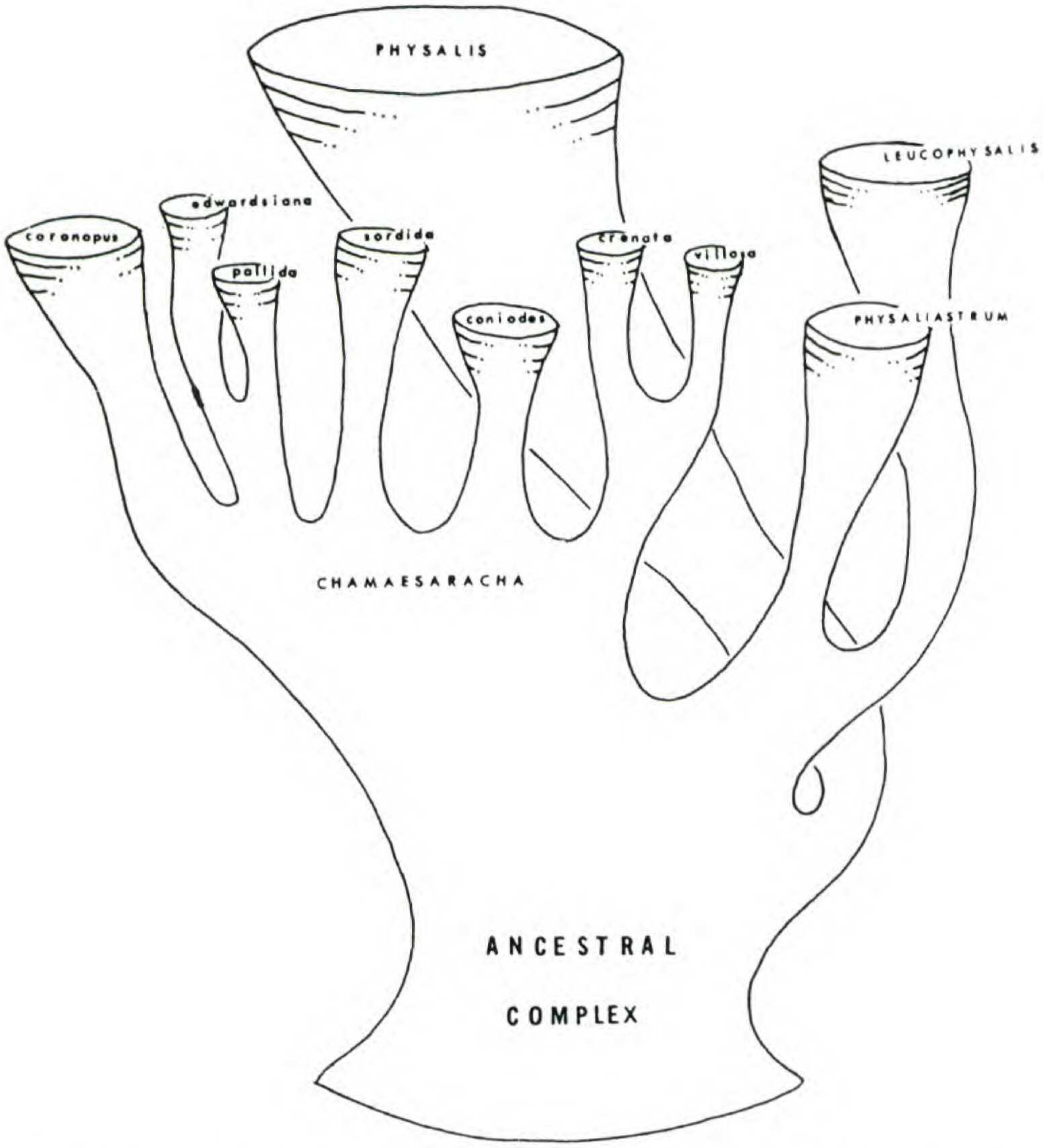

Figure 1. Hypothetical phyletic relationships within *Chamaesaracha*.

of the species of *Chamaesaracha* (Figure 1). While the diagram is highly conjectural from a phyletic point of view, it nonetheless expresses visually my views on the relationships among the taxa.

The flavonoid chemistry of the various species of the genus supports the relationships suggested in Figure 1. In what are considered to be advanced taxa, there is a general decrease of O-glycosylation and O-methylation, presumably reflecting the loss of enzymes necessary for these substitutions. In addition, the more closely related taxa (as I have grouped them) do have a greater similarity in their chromatographic profiles.

ACKNOWLEDGMENTS

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TAXONOMIC TREATMENT

Chamaesaracha Gray

Chamaesaracha A. Gray, Bot. Calif. 1:540, 1876. TYPE SPECIES: *Chamaesaracha coronopus* (Dunal) Gray.

Saracha Ruiz & Pav. sec. Chamaesaracha Gray, Proc. Amer. Acad. **10**:62. 1874.

Rhizomatous perennial herbs; stems erect, ascending, or prostrate, 10-50 cm long, much branched, round striate or angular; glabrous to variously pubescent; leaves simple, broadly ovate, ovate, rhomic, lanceolate, oblanceolate, or linear-lanceolate, entire to pinnately or irregularly lobed, subsessile to distinctly petiolate, base attenuate to truncate, apex acute, rounded, or obtuse with veins prominent or obscure; flowers 1-5 in axils, pedicels slender, elongating and becoming curved or twisted in fruit; calyx campanulate, rounded at the base, connate ¼-¾ its length, pubescent; corolla repand-rotate, white, ochroleuceous, or yellow-green, often tinged with purple on the outer surface of the lobes, with white tomentose appendages in the throat; stamens inserted near the base of the corolla; filaments slender, ca 3 mm long, anthers yellow, ca. 1.5 mm long, dehiscing longitudinally; styles slender and somewhat curved; stigmas blunt, or minutely 2-cleft; fruit a globose berry, tightly invested, but not enclosed, by the accrescent calyx; seeds flattened, reniform, rugose-reticulate, browning with maturity; $x = 12$.

KEY TO THE SPECIES

a. Leaves 1.5-3.5 cm wide, ovate to broadly ovate-lanceolate, entire to crenate; flowering calyces exceeding 5mm long. . . . . *b.*
  b. Herbage villous with long forked and simple trichomes; leaves subsessile, blades ca ½ as wide as long. . . . . 4. *C. villosa.*
  b. Herbage basically glandular-pubescent, but with some longer simple trichomes; leaves petiolate, blades ca as wide as long. . . . . 5. *C. crenata.*
a. Leaves less than 2.0 cm wide; flowering calyces usually less than 4 mm long. . . . . *c.*
  c. Herbage predominately glabrous or pubescent with branched or stellate hairs; leaves linear, linear-lanceolate, or rhombic, entire irregular, or few-lobed; stems usually purplish or gray at base. . . *d.*
    d. Leaves linear to linear-lanceolate, usually few-lobed; sparsely pubescent with scurfy, white, stellate or branched hairs. . . . . . *e.*
      e. Leaves sparsely pubescent with stellate hairs; pedicels without glandular hairs. . . . . 1. *C. coronopus.*

- *e.* Leaves glabrous; pedicels with glandular hairs. . . . . 2. *C. edwardsiana.*
- *d.* Leaves broadly lanceolate to rhombic, subentire or entire, pubescent with stellate hairs. . . *f.*
  - *f.* Leaves densely pubescent with stellate hairs. . . . . 3. *C. pallida.*
  - *f.* Leaves glabrous. . . . . . . 2. *C. edwardsiana.*
- *c.* Herbage predominately glandular-pubescent or glandular-pubescent mixed with simple, longer trichomes; leaves broadly lanceolate or rhombic, entire to pinnately or irregularly lobed; stems green. . . . . *g.*
  - *g.* Pubescence of short glandular hairs. . . . . 6. *C. sordida.*
  - *g.* Pubescence of trichomes mixed with glandular hairs. . . . . 7. *C. coniodes.*

1. **Chamaesaracha coronopus** (Dunal) Gray, Bot. Calif. 1:540. 1876. Holotype (G!), Mexico, ca Laredo: [Texas, Webb Co. near Laredo] *Berlandier* 1494. Isotypes: not seen. Fig. 2.
Solanum coronopus Dunal, in DC. Prod. 13:54. 1852.
Saracha coronopus (Dunal) Gray, Proc. Amer. Acad. **10**:62. 1874.

Rhizomes slender and subligneous, 1.5-3.5 mm in diameter; stems prostrate or ascending, 10-50 cm long, ca 1.5 mm in diameter, usually purplish or grey below; herbage glabrous to sparsely pubescent with scurfy, short, white stellate hairs; leaves linear to linear-lanceolate, 2.0-6.5 cm long, 1-10 (-15) mm wide, gradually narrowing to an attenuate, subsessile base, apex of blade acute, rounded, or obtuse, midrib prominent, sparsely pubescent with stellate hairs, margin subentire to deeply lobed; flowers 1 or 2 in axils; calyx 2.5-4.0 mm long, rather densely pubescent; corolla 6-10 (-15) mm wide; fruit 4-8 mm in diameter; chromosome number, $n = 12, 24, 36$.

A rather widespread, weedy species occurring throughout most of the range of the genus (Fig. 3). At various

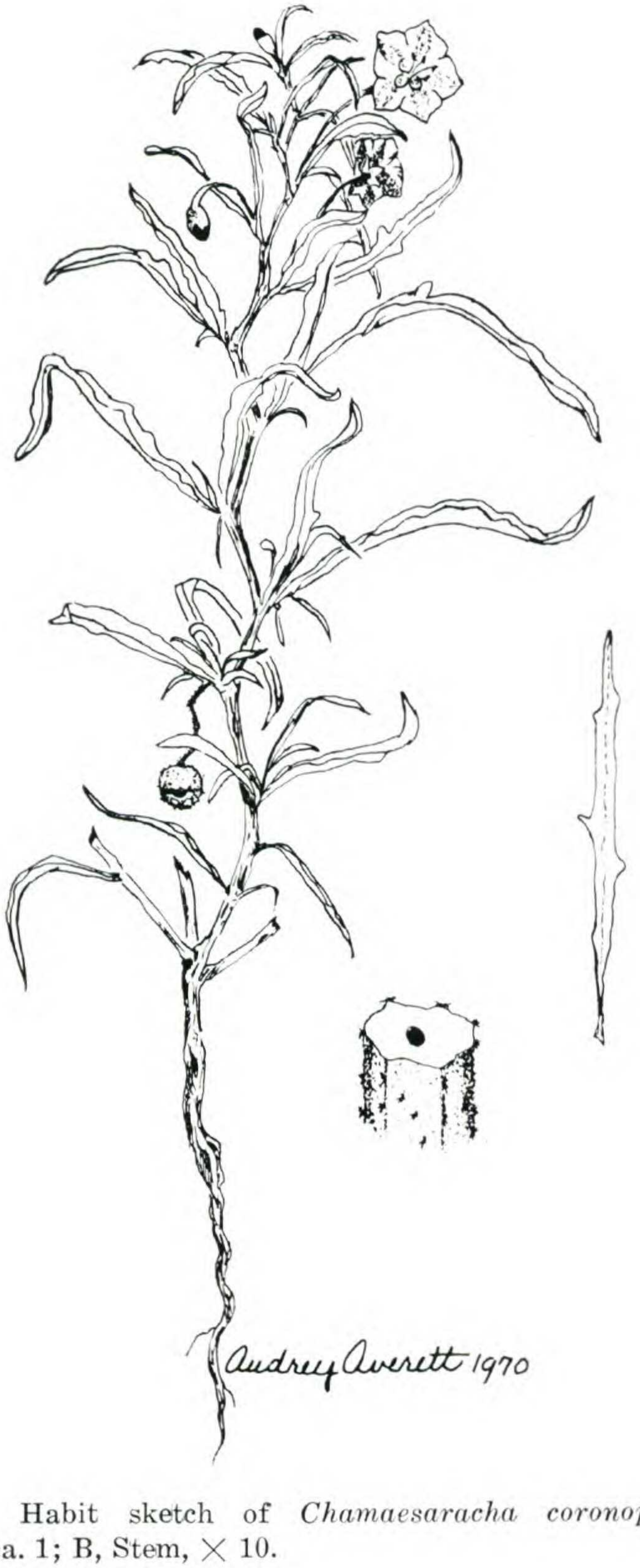

Figure 2. Habit sketch of *Chamaesaracha coronopus*, × 1; A, Leaf, × ca. 1; B, Stem, × 10.

elevations from sea level to 7000 ft., but more frequently in grassland areas with *Larrea, Prosopis,* and *Juniperus,* the species does not seem to be restricted to particular soil types and has even been collected on gypseous soils. Flowering from March to October, primarily in the early and again in the later summer, depending on rains.

Chamaesaracha coronopus is most closely related to *C. edwardsiana.* The plants from south Texas differ somewhat from those found in west Texas, New Mexico, and Arizona in having broader, more lobed leaves. In leaf shape, the plants from south Texas superficially resemble *C. coniodes,* but the two species are not believed to be closely related.

REPRESENTATIVE SPECIMENS: **Arizona:** APACHE CO. Window Rock, 19 Aug 1962. *Bohrer* 737 (UC). COCHISE CO. Ft. Lowell, 31 Jul 1903, *Thomber* 245 (ARIZ, NY, UC). COCONINO CO. Black Point, near Cameron, 18 May 1961, *Demaree* 44084 (ARIZ, SMU, UC). GILA CO. 16 mi S of Safford, 21 Oct 1964, *Gould* 3989 (ARIZ, UC). MOHAVE CO. 5 mi NE of Tweep, *Parker et al.* 6256 (ARIZ, US). NAVAJO CO. Holbrook, 27 Jun 1896, *Zuck s.n.* (GH, NY, US). PIMA CO. Vail, 22 Oct 1926, *Peebles et al.* 3306 (ARIZ, MICH). PINAL CO. near Sacaton, 2 May 1926, *Harrison* 1779 (ARIZ). LAVAPAI CO. near Montezuma Castle Nat'l Monument, 21 May 1936, *Nelson & Nelson* 2050 (GH, NY, UC). YUMA CO. Antelope, May-Oct 1902, *Purpus* 95 (UC).

Colorado: FREEMONT CO. Canyon City, 1872, *Brandegee* 391 (GH, NY, UC, US). LAS ANIMAS CO. 10 mi N of Bronson, 16 Jul 1968, *Averett & Tomb* 348 (SMU, MO, TEX). LINCOLN CO. 7 mi S of Forder School, 6 Jul 1937, *Ownbey* 1327 (GH, NY, UC). PUEBLO CO. mesas near Pueblo, 15 May 1900, *Rydberg & Vreeland* 5666 (NY).

Oklahoma: CIMARRON CO. 3.5 mi N of Kenton, 7 Oct 1950, *Waterfall* 9713 (ARIZ, OKLA, SMU).

New Mexico: BERNALILLO CO. Albuquerque, 4 Sep 1884, *Jones* 4147 (ARIZ, GH, NY, UC, US). COLFAX CO. vicinity of Raton, 21-22 Jun 1911, *Standley* 6365 (US). DONA ANA CO. plains E of Organ mts. 28 Aug 1897, *Wooton* 406 (GH, NY, UC, US). GRANT CO. Mangas Springs, 18 mi NW of Silver City, 31 May 1903, *Metcalfe* 97 (ARIZ, NY, UC, US). HIDALGO CO. 5 mi N of Animas, 9 Sep 1950, *Castetter* 3030 A & B (UNM). LINCOLN CO. above Tularosa, 24 Aug 1897, *Wooton s.n.* (ARIZ, US). LUNA CO. foothills, Tres Hermanas Mts, W of Columbus, 12 Sep 1942, *Clark s.n.* (UNM). MCKINLEY CO. Gallup, 28 Jul 1933, *Degener* 4834 (NY). OTERO CO. White Mts, divide above Mescalero, 1 Aug 1897, *Wooton s.n.* (NY, US). SANDOVAL CO. 19 mi W of Santa Fe on Rio Grande River, 31 May 1897, *Heller & Heller* 3633 (GH,

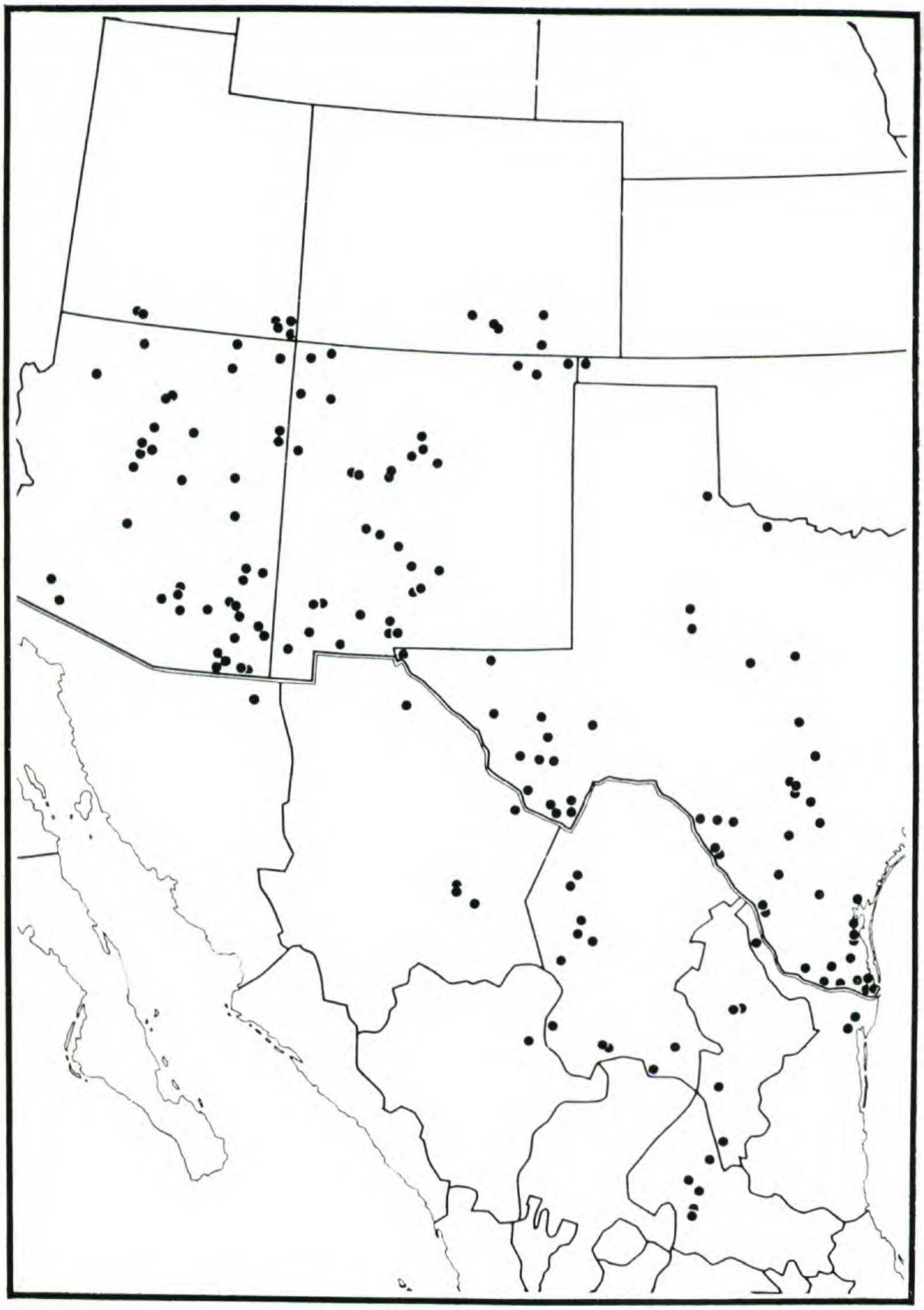

Figure 3. Distribution of *Chamaesaracha coronopus*.

NY, US). SAN JUAN CO. Sheep Springs, 18 Aug 1880, *Rusby* 302 (MICH, NY). SAN MIGUEL CO. near Pecos, 18 Aug 1908, *Standley* (GH, NY, US). SANTA FE CO. S of Santa Fe near hwy 85, 14 Jul 1966, *Plowman* AP195 (ARIZ). SOCORRO CO. Ojo Caliente, 28 Jul 1904, *Wooton* 2683 (US). UNION CO. 2 mi W of Oklahoma line, NW of Kenton, 11 Jun 1948, *Rogers* 5973 (MICH, US). VALENCIA CO. 5 mi W of Correo, 15 Jun 1959, *Martin* 3273 (UNM).

Texas: BEXAR CO. San Antonio, 23 Apr 1917, *Palmer* 11626 (TEX). BREWSTER CO. Alpine, 7 Jun 1940, *Warnock* 21586 (TEX). BROWN CO. Brownwood, 31 Mar 1917, *Palmer* 11439 (TEX). BURNET CO. Marble Falls, 1 Apr 1913, *Young s.n.* (TEX). CAMERON CO. Boca Chica rd, 2 mi E of Palmito battleground monument, 29 Apr 1959, *Travers* 1160 (SMU, TEX). CHILDRESS CO. Spr 1931, *Biology class s.n.* (TEX). CULBERSON CO. railroad near Kent, 1 May 1902, *Tracy & Earle* 407 (NY, TEX, US). DUVAL CO. San Diego, 1885, *Croft* 5994 (US). EL PASO CO. vicinity of El Paso, 1911, *Stearns* 39 (US). ERATH CO. 21 Mar 1921, *Gough s.n.* (TEX). HIDALGO CO. 6 mi E of Sulivan City, 8 Mar 1959, *Turner* 4493 (TEX). JEFF DAVIS CO. 9 mi NE of Ft. Davis in Limpia Canyon, 27 Apr 1947, *Cory* 53554 (SMU). KARNES CO. 0.5 mi NW of Karnes City, 14 Mar 1953, *Johnson* 1140 (SMU, TEX). KLEBERG CO. Kingsville, 11 Apr 1905, *Tracy* 9225 (GH, NY, TEX, US). LA SALLE CO. 10 mi N of Encinal, 30 Mar 1935, *Wiegand* 2065 (GH). MAVERICK CO. on the Rio Grande River, Eagle Passs, 7 Mar 1852, *Schott s.n.* (NY, US). MCKINNEY CO. 1881, *Garrett s.n.* (NY). MITCHELL CO. 5 mi SE of Colorado City, 29 Jul 1945, *Pohl* 5113 (SMU). NUECES CO. Corpus Christi 21 Mar 1907, *York s.n.* (TEX). OLDHAM CO. Tascosa, 16 Jun 1932, *Reed* 3510 (US). PECOS CO. 3 mi N of Ft. Stockton, 22 Jun 1952, *Warnock* 10490 (SMU). PRESIDIO CO. Marfa, Jun 1936, *Hinckley* 658 (ARIZ, GH, SMU, TEX). SAN PATRICIO CO. 8 mi E of Taff, 20 Oct 1951, *Jones* 652 (SMU). SCURRY CO. 26 mi SW of Snyder, 17 Apr 1960, *Waterfall* 15875 (OKLA). STARR CO. 4 mi W of Ft Ringold, *Tharp & York* 51-250 (TEX). TAYLOR CO. 8 mi S of Abilene, 8 Apr 1960, *McCoy* 3727 (OKLA). TRAVIS CO. Austin, 18 Mar 1940, *Warnock* 88 (TEX). UVALDE CO. NW of Uvalde, 3 Apr 1942, *Lundell & Lundell* 10974 (SMU, US). VAL VERDE CO. Del Rio, 7 Dec. 1891, *Plank s.n.* (NY). WEBB CO. Laredo, 1-20 Aug 1879, *Palmer* 920 (GH, NY). WICHITA CO. 215 mi W 1 mi S of Iowa Park, 8 Jun 1960, *Mahler* 1168 (TEX). WILLACY CO. 3 mi S of Raymondville, 6 Nov 1953, *Shinners* 17108 (SMU). WILSON CO. 4 mi S of Stockdale, 25 Mar 1955, *Johnston & McCart* 5082 (TEX).

Utah: KANE CO. 8 mi E of Kanab, 7 Jun 1957, *Anderson* 760 (NY, UC). SAN JUAN CO. along the San Juan River, 20-25 Aug 1911, *Rydberg & Garrett* 9970 (NY, US).

Mexico: CHIHUAHUA, 6 mi S of Camargo, 29 Jun 1937, *Shreve* 8070 (ARIZ, GH, US). COAHUILA, Saltillo and vicinity, 1898, *Palmer* 145 (GH, NY, UC, US). DURANGO, 85 mi NE of Durango, 11 Aug 1959,

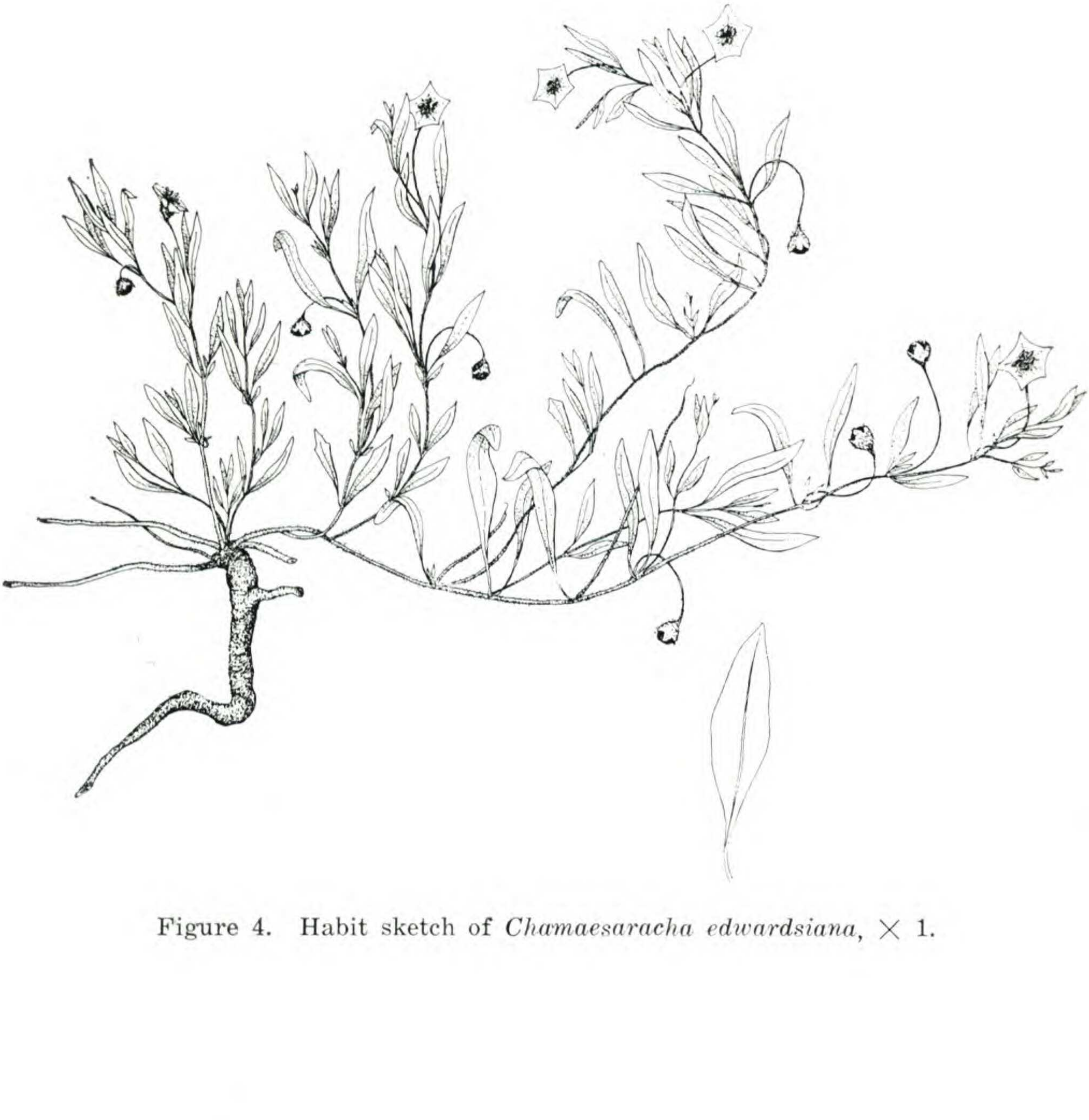

Figure 4. Habit sketch of *Chamaesaracha edwardsiana*, × 1.

Waterfall 15399 (OKLA). NUEVO LEON, 16 mi N of Matehuala, 21 Aug 1959, *Waterfall* 15749 (OKLA). SAN LUIS POTOSI, San Luis Potosi, 1879, *Shaffner* 404 (NY, US). SONORA, mesa de las Carreras, W of Colonia Morelos, 15 Sep-4 Oct 1941, *White* 4547 (ARIZ, GH, MICH). TAMAULIPAS, 10 mi S of Nuevo Leon, 26 Feb 1944, *Barkley* 14326 (GH, NY, TEX).

2. **Chamaesaracha edwardsiana** Averett, Sida 5: 48-49. 1972. Holotype (TEX): TEXAS, Travis Co.: ½ mi E of the Pedernales River on hwy 620. 28 Jun 1968. *Averett* 289. Isotypes: GH, MO, SMU. (Fig. 4).

Rhizomes slender and subligneous, 1.5-3.5 (-7) mm in diameter; stems erect or ascending, 7-30 cm long, ca 1.5 mm in diameter, usually purplish or grey below; herbage glabrous to pubescent with stellate hairs, or occasionally with simple and branched trichomes (especially in the upper portions); leaves linear-lanceolate to rhombic, typically undulate, but occasionally few-lobed, 2.5-7.0 cm wide, base attenuate, subsessile to slightly petiolate, midrib prominent, but secondary veination usually present, essentially glabrous; flowers 1 or 2 in axils, flowering pedicel pubescent with trichomes and glandular hairs; calyx 4-5 mm long, pubescent with stellate, branched and simple trichomes; corolla 1.0-1.5 cm wide; fruit 5-8 mm in diameter; chromosome number, $n = 24$.

Primarily on limestone soils in the Edwards Plateau of Texas (Fig. 6). Flowering from March to October, but mostly in the early and late summer, depending on rains.

Chamaesaracha edwardsiana is probably most closely related to *C. coronopus*, differing from the latter in having glabrous, entire leaves. It is also related to *C. pallida*, differing in the narrow, linear-lanceolate, glabrous leaves.

REPRESENTATIVE SPECIMENS: **Texas:** BEXAR CO. near Bracken, 13 Jul 1903, *Groth* 73 (GH, US). BLANCO CO. ca 1 mi W of Johnson City, 5 Apr 1969, *Tomb & Tomb* 386 (TEX). BRAZOS CO. ½ mi from A & M Campus, College Station, 26 Apr 1967, *Lonard* 1899, (TEX). COMAL CO. Comanche Springs, New Braunfels, May, 1850, *Lindheimer* 1938 (ARIZ, GH, NY, SMU, TEX, UC, US). CROCKETT CO. McKenzie's Well, May 188?, *Reverchon* 1569 (NY, SMU, US). EDWARDS CO. Ranch Expt. Sta., 2 Nov 1929, *Cory* 3469 (GH). HAYS CO.

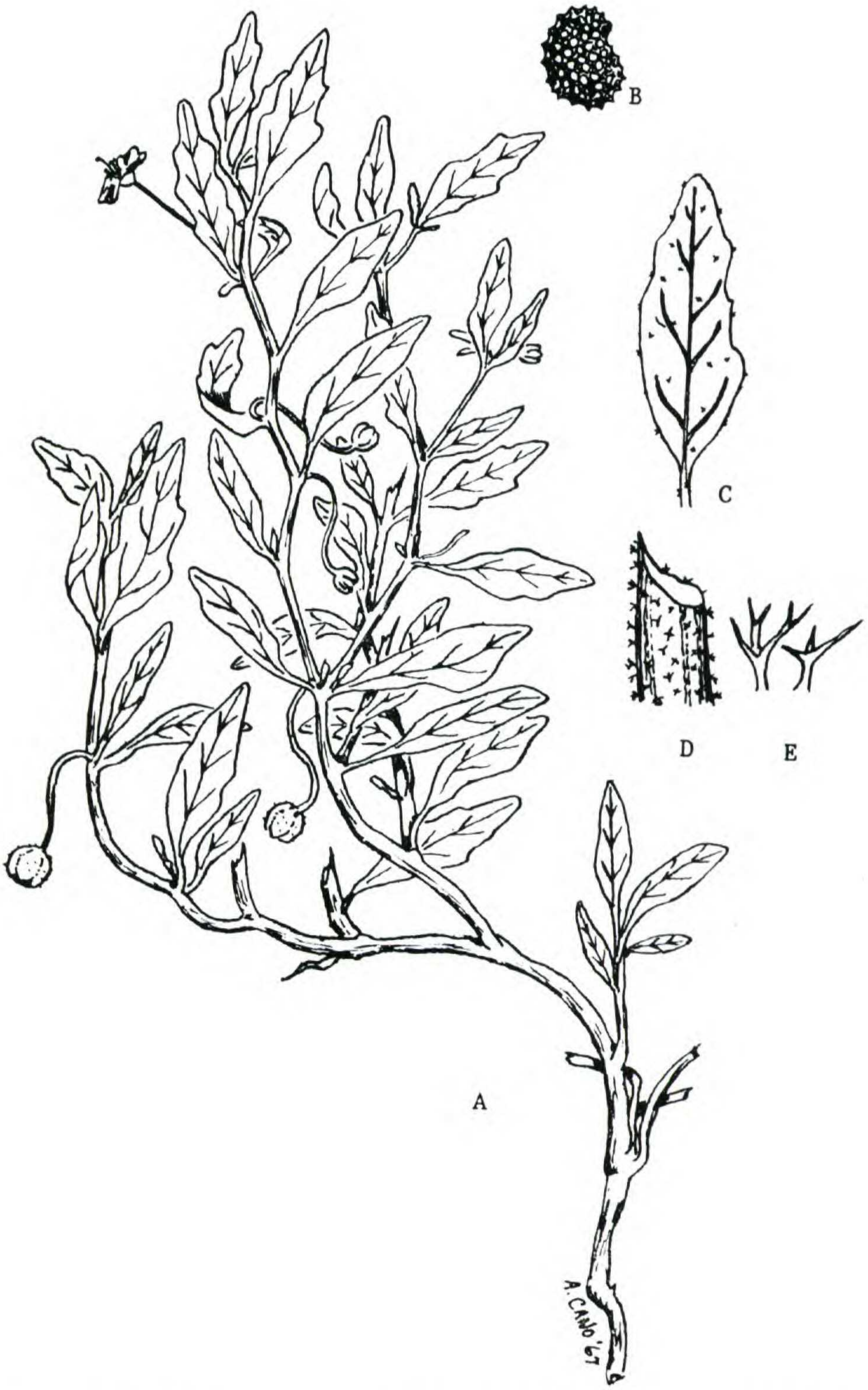

Figure 5. *Chamaesaracha pallida:* A, Habit sketch, × 1; B, Seed, × ca. 5; C, Leaf × 2; D, Stem, × ca. 10; E, Pubescence, × 50.

E of Henly, 20 Apr 1941, *Lundell & Lundell* 10279 (MICH, US). LAMPASAS CO. 8 mi E of Lampasas, 15 Jun 1929, *Wolff* 940 (US). LLANO CO. near Llano, 4 Aug 1931, *Wolff* 3080 (US). KENDALL CO. 5 mi N of Boerne, 10 May 1969, *Averett* 454 (SMU, MO, TEX). KERR CO. Kerville, 19-25 Apr 1894, *Heller* 1647 (ARIZ, GH, MICH, NY, SMU, UC, US). MENARD CO. 5 mi NE of Menard, 3 Jun, 1968, *Shinners* 32274 (SMU). PECOS CO. 15 mi W of Sanderson, 22 Apr 1948, *Whitehouse* 19729 (MICH, NY, OKLA, SMU). TRAVIS CO. Austin, 17 May 1940, *Lundell & Lundell* 8957 (GH, MICH, NY, SMU, UC, US). UVALDE CO. Montell, 15 Oct 1917, *Palmer* 13006 (TEX, UC). WEBB CO. Laredo Junior College Pasture, 14 Apr 1963, *Abrego s.n.* (TEX). WILSON CO. Sutherland Springs, Aug 1879, *Palmer s.n.* (GH). WILLIAMSON CO. SW of Georgetown, 16 May 1942, *Wolcott* 118 (TEX).

Mexico: COAHUILA, Sierra del Pinto, 26 Aug 1940, *Johnston & Muller* 745 (GH, MICH). NUEVO LEON, 10 mi S of Roberto Junction on hwy 56, 22 Jul 1969, *Bierner & Turner* 90 (TEX). SAN LUIS POTOSI, Charcas, Jul-Aug 1934, *Lundell* 5065 & 5065A (ARIZ, MICH, OKLA, TEX, US).

3. **Chamaesaracha pallida** Averett, Sida 5: 48-49. 1972. Holotype (TEX): TEXAS, Presidio Co.: 35 mi SW of Marfa on Pinto Canyon Road. 15 Jul 1966. *Averett* 155. Isotypes: GH, MO, SMU, US. Fig. 5.

Rhizomes slender and subligneous, occasionally woody; stems suberect to ascending, 7-15 (-20) cm long, 1.0-1.5 cm wide (ca ½ the length), narrowly rhombic, broadly lanceolate, or oblanceolate, entire to deeply undulate, apex acute, obtuse, or rounded, base attenuate, subsessile or short-petiolate, pubescent with stellate or branched hairs; flowers 1 or 2 in axils, pedicels slender 1-2 cm long; calyx 3-4 mm long, pubescent; corolla usually 1-1.5 cm wide; fruit 5-7 mm in diameter; chromosome number, $n = 36$.

A rather rare species of Trans-Pecos, Texas and northern Mexico (Figure 6). Flowering from March to October, primarily in the early and late summer depending on rains. The species appears to be mostly confined to limestone soils, although it has been reported from igneous soils.

Chamaesaracha pallida has its closest affinities with *C. edwardsiana,* and to some extent, *C. sordida.* However, a dense stellate pubescence is typically found in *C. pallida.*

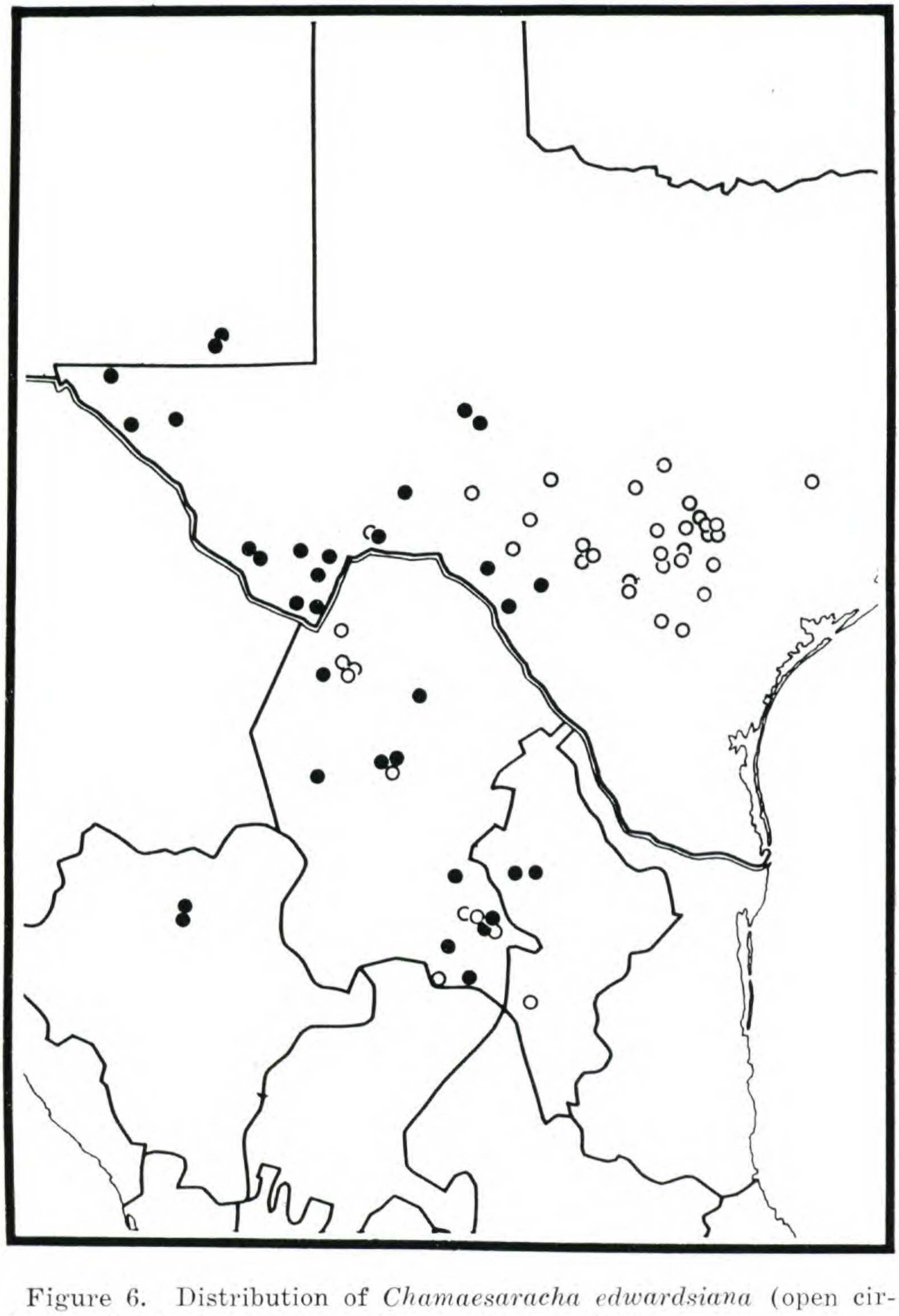

Figure 6. Distribution of *Chamaesaracha edwardsiana* (open circles) and *Chamaesaracha pallida* (closed circles).

Some specimens of *C. edwardsiana* and *C. coronopus* may have considerable pubescence, but not so much as *C. pallida.*

REPRESENTATIVE SPECIMENS: **New Mexico:** EDDY CO. Sitting Bull Falls, 24 May 1944, *Hershey* 3098 (GH).

Texas: BREWSTER CO. 30 mi S of Marathon, 2 Apr 1938, *Warnock* T283 (TEX, US). CULBERSON CO. S of McKittrick Canyon, Guadalupe Mts, 3 Aug 1952, *Warnock* 10941 (SMU). EL PASO CO. Hueco Pass, 29 May 1932, *Whitehouse s.n.* (TEX). HUDSPETH CO. Calcareous Canyon, Malone Mts, 21 Aug 1946, *Waterfall* 6663 (GH, NY). IRION CO. 1 mi S of Mertzon, 24 Apr 1948, *Warnock* 7700 (TEX). KIMBLE CO. 16 Apr 1930, *Wolff* 1601 (US). KINNEY CO. Anacacho Mts, ca 30 mi SE of Brackettville, 15 May 1965, *Strother* 253 (TEX, SMU). PECOS CO. ca 15 mi W of Sanderson, 22 Apr 1948, *Whitehouse* 19729 (SMU). PRESIDIO CO. 3 mi SW of Shafter, 30 Jul 1945, *Muller* 8471 (NY, OKLA, SMU). REGAN CO. 7⅓ mi E of Bit Lake, 24 Apr 1947, *Cory* 53440 (NY, SMU). TERRELL CO. Blackstone Ranch, ca 15 mi S of Sheffield, 15 Jun 1949, *Webster* 269 (MICH, TEX). TOM GREEN CO. 7⅔ mi S of Christoval, 28 Oct 1945, *Cory* 50565 (GH, NY, SMU, UC, US). UVALDE CO. 4 mi E of Kline, 2 Nov 1963, *Moore et al.* 8845 (SMU). VAL VERDE CO. 30 (airline) mi N of Del Rio, 25 Apr 1943, *Cory* 41528 (GH).

Mexico: COAHUILA, 26 mi SW of Monterrey, 1 Dec 1945, *Barkley & Warnock* 14700M (GH, NY, TEX). DURANGO, 9 mi N of La Zarca on hwy 45, *Sikes & Patterson* 398A,B,C, (SMU, SRSC, TEX). NUEVO LEON, Villa de Garcia, 19 Sep 1959, *Fuentes* 19 (OKLA).

4. **Chamaesaracha villosa** Rydb., Mem. Torr. Bot. Club 4: 368. 1896. Holotype (US!), MEXICO, Coahuila: mountains 24 mi NE of Monclova. Sept 1880. *Palmer* 924. Isotypes: GH!, K!, NY!, US!, VT!. Fig. 7.

Plants strongly perennial; rhizomes woody, stems suberect to ascending, 15-50 cm long, 1.5-3.5 mm in diameter, herbaceous to somewhat woody, densely pubescent with long, villous, forked trichomes, occasionally somewhat glandular; leaves 4-7 cm long, 1.5-3.0 cm wide, ovate to ovate-lanceolate, entire to undulate-crenate, apex acute to obtuse, base attenuate, petioles less than ¼ the total length of the leaf if present; flowers 1 to few in axils; pedicels 1-3 cm long; calyx ca 5 mm long, pubescent; corolla 0.5-3.0 cm wide; fruit 5-8 mm in diameter; chromosome number, *n*-12.

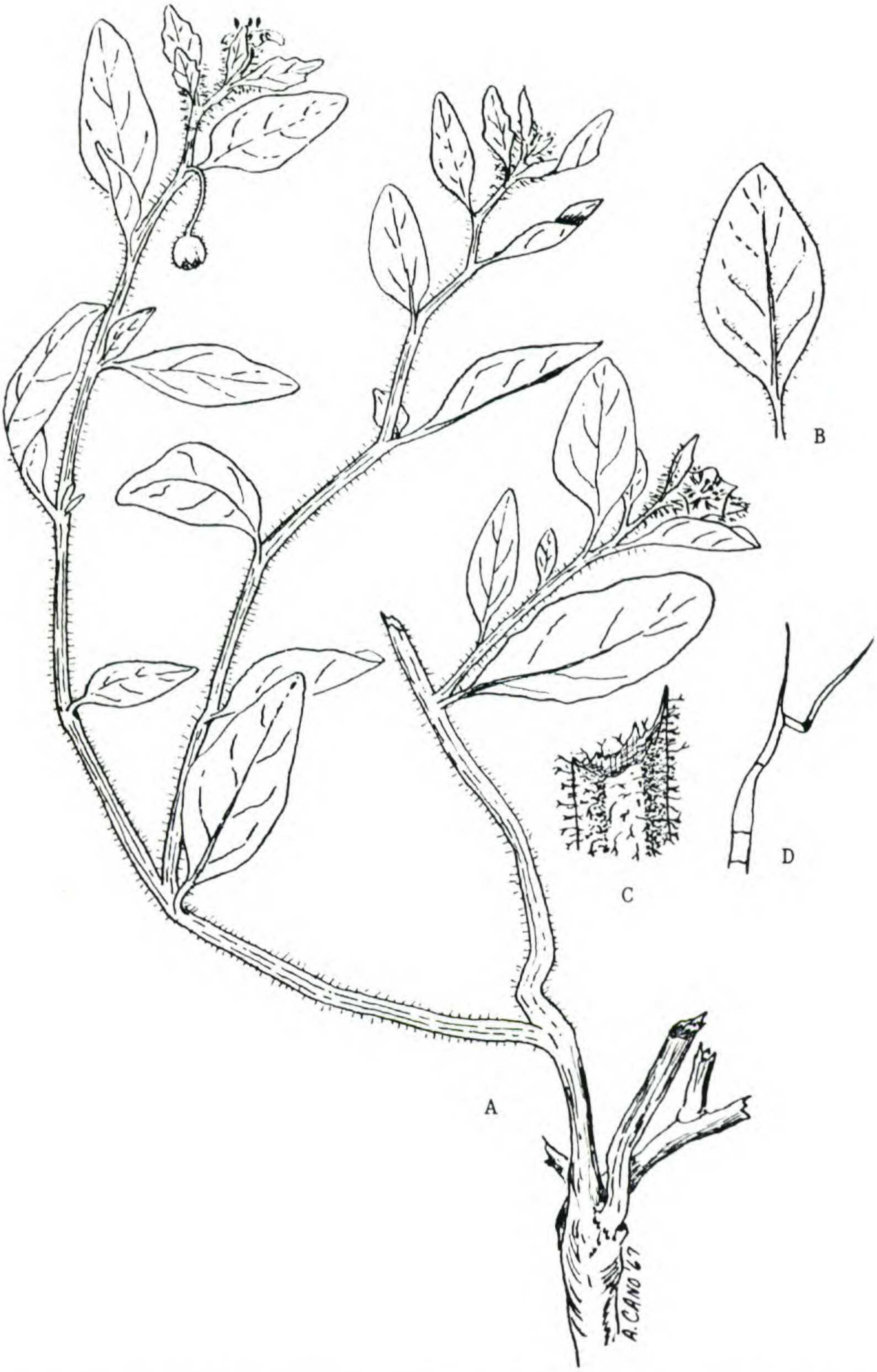

Figure 7. *Chamaesaracha villosa:* A, Habit sketch, × 1; B, Leaf, × 1; C, Stem, × 10; D, Pubescence, × 40.

Creosote bush dominated desert areas of northern Mexico (Durango, Chihuahua, and Coahuila) and Trans-Pecos Texas along the Rio Grande River (Fig. 9), usually occurring in sandy or gravelly washes or along the roadside in disturbed areas. Flowering primarily in early spring (March-April) and fall (September-October).

Considerable data indicate that *Chamaesaracha villosa* is most closely related to *C. crenata*. Further discussion of the two species is found following treatment of the latter.

REPRESENTATIVE SPECIMENS: **Texas:** BREWSTER CO. near Comanche Springs between Terlingua and Lajitas, 17 Jul 1937, *Warnock* 20701 (TEX). CULBERSON CO. N of Van Horn, 10 Jun 1905, *Reverchon s.n.* (SMU). HUDSPETH CO. Indian Hot Springs, 20 Apr 1932, *Whitehouse* 8500 (TEX). PRESIDIO CO. 5 mi N of Ruidosa, 26 May 1964, *Scudday* 372 (OKLA, SRSC).

Mexico: CHIHUAHUA, 31 mi N of Jimenez, 1 Aug 1939, *White* 2171 (ARIZ, GH, MICH). COAHUILA, Mohano, Jun 1910, *Purpus* 4550 (GH, UC, US). DURANGO, 2 mi W of Bermejillo, 18 Sep 1938, *Shreve* 8783 (ARIZ, MICH, UC).

5. **Chamaesaracha crenata** Rydb., Mem. Torr, Bot. Club 4: 368. 1896. Holotype (US!), MEXICO, Coahuila: Parras, 111 mi W of Saltillo. Jun 1880. *Palmer* 923. Isotypes GH!, K!, NY!, US!, VT!. Fig. 8.

Plants strongly perennial; rhizomes woody; stems 15-40 cm long, 1.5-3.5 mm in diameter, herbaceous or somewhat woody, much branched, densely pubescent with glandular hairs mixed with longer trichomes; leaves 4-6 cm long, 1.5-3.5 cm wide, ovate to broadly rhombic, entire-undulate to crenate, apex obtuse, base cuneate or somewhat attenuate; petioles 2-3 cm long (ca 1/3 the total length of the leaf); flowers 1-5 in axils: pedicels 1-3 cm long; calyx (3-) 5-7 mm long, densely pubescent, primarily with long trichomes; corolla 1-2 cm wide; fruit 8-10 mm in diameter; chromosome number, $n = 12$.

Creosote-desert shrub areas of northern Mexico and along the Rio Grande River in Texas (Fig. 9). Usually found in sandy or gravelly washes or along the roadside in

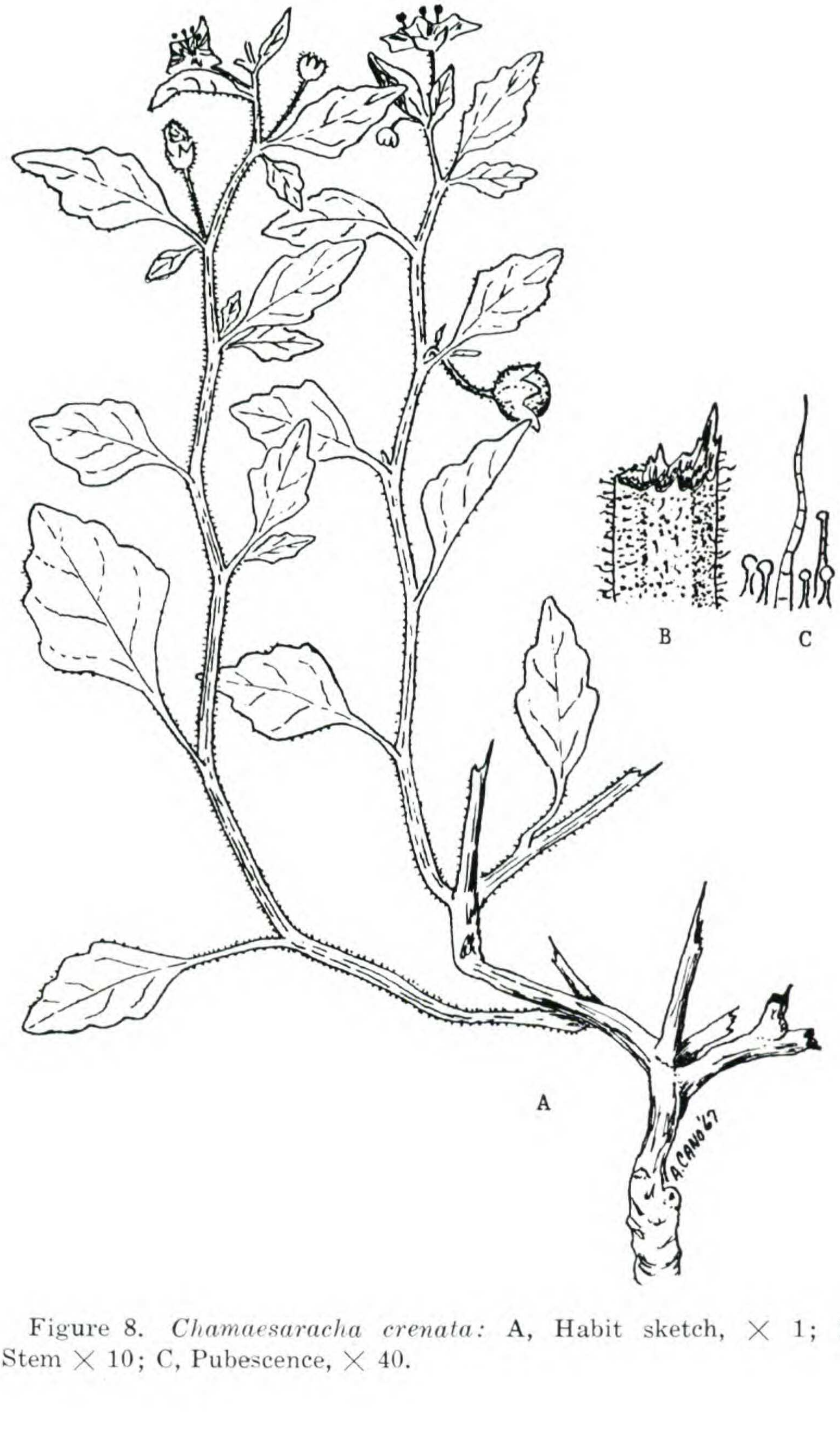

Figure 8. *Chamaesaracha crenata:* A, Habit sketch, × 1; B, Stem × 10; C, Pubescence, × 40.

disturbed areas. Flowering primarily in early spring and in the fall, depending on rains.

Chamaesaracha crenata is most closely related to *C. villosa*. The two species are largely allopatric, but their ranges overlap in Coahuila and in the Trans-Pecos area of Texas (Figure 9). In the latter area, particularly in Big Bend National Park and around Lajitas (Brewster and Presidio Co), the two species are often difficult to distinguish and hybridization is suspected. At the extremities of their ranges, however, the two species are fairly clear and they can be distinguished by the characters given in the key to the species.

Rydberg, in distinguishing the two species, used differences in flower size, fruit size, seed number, and calyx shape. The type specimens do exhibit such differences; however, they are not particularly useful in distinguishing between the taxa since these characters are quite variable both within and among populations.

I have maintained the species as distinct for biological reasons although it might be equally sound to treat the taxa as varieties of but a single species. The characters that distinguish the two are largely of the same kind that distinguish other species in the genus (viz., leaf shape and pubescence), although, perhaps because of gene exchange in regions of overlap, the differences are often not so easily seen. The decision for varietal or specific status is somewhat arbitrary in this instance, so I have chosen to follow Rydberg's treatment in recognizing allopatric species showing minimal gene exchange in regions of sympatry.

REPRESENTATIVE SPECIMENS: **Texas:** BREWSTER CO. Glenn Springs, Big Bend Nat'l Park, 25 May 1955, *Warnock & Wallmo* 12300 (SRSC, TEX). STARR CO. 3 mi N of Roma, 31 Jan 1954, *Shinners* 17714 (SMU). TERRELL CO. Feodora, 26 Apr 1928, *Palmer* 33582 (GH, NY, US). VAL VERDE CO. Shumla, 10 Oct 1936, *Tharp, s.n.* (GH, NY, SMU, UC, US). WEBB CO. Laredo, 15 Mar 1917, *Palmer* 11285 (UC).

Mexico: CHIHUAHUA, 5 km W of Santa Fe, 15 Sep 1942, *Stewart* 2604 (GH). COAHUILA, Parras, Mar 1905, *Purpus* 1081 (GH, NY, UC).

6. *Chamaesaracha sordida* (Dunal) Gray, Syn. Fl. N.

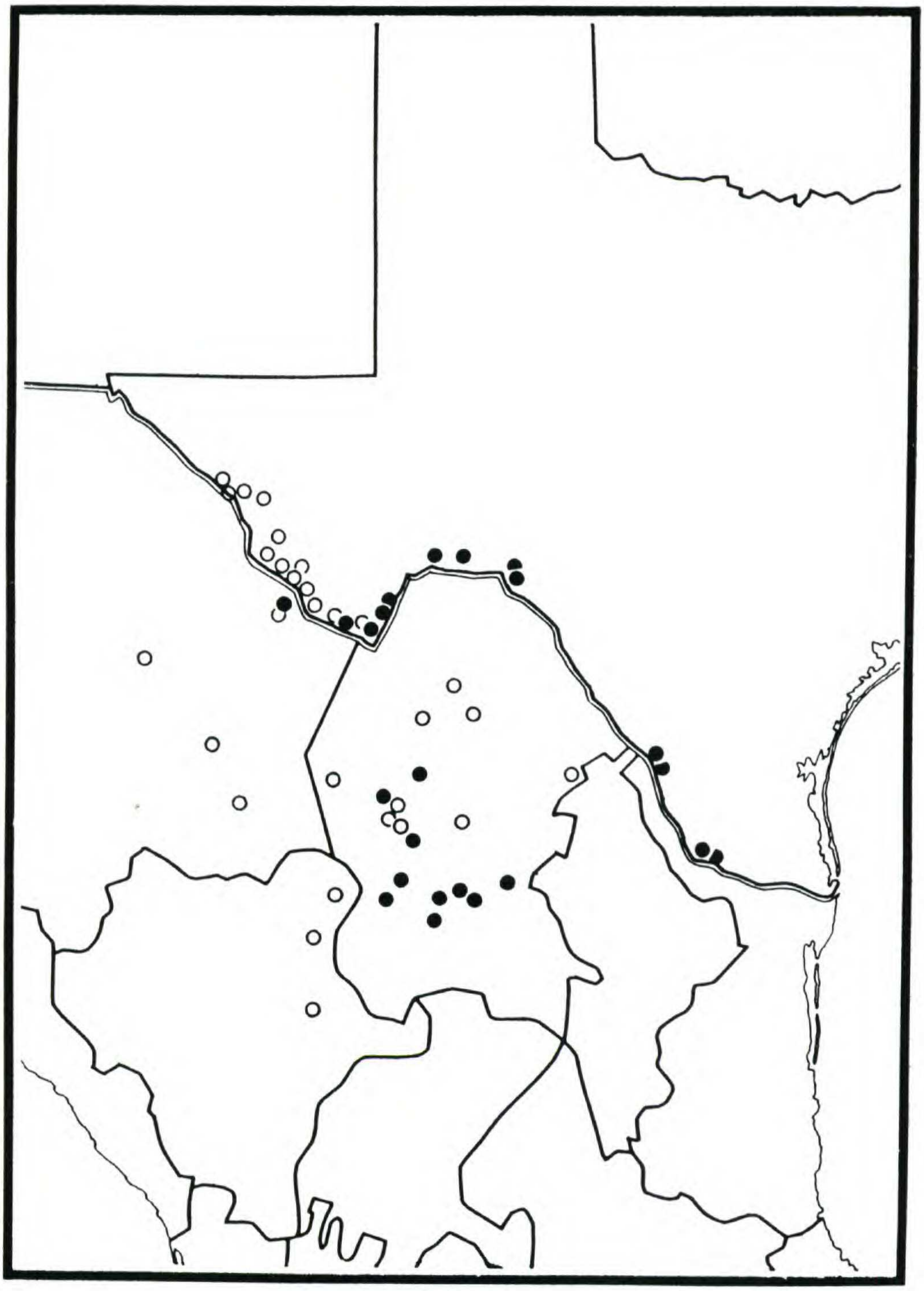

Figure 9. Distribution of *Chamaesaracha villosa* (open circles) and *Chamaesaracha crenata* (closed circles).

Amer. **1**: 232. 1876. Holotype (G!), tracing (GH!): TEXAS: Webb Co. near Laredo, Aug 1829. *Berlandier* 2076 (=666). Isotypes: GH!, NY(2)!. Fig. 10.
Withania sordida Dunal. in D.C. Prod. 13: 456. 1852.

Rhizomes subligneous to woody; stems suberect to ascending, 9-30 cm long (typically ca 15 cm), 1.5-2.0 mm in diameter, pubescent, herbage densely glandular pubescent, occasionally mixed with simple trichomes; leaves rhombic, entire or subentire to only slightly lobed, 1.5-4.0 cm long, 4-8 (-10) mm wide, acute to somewhat rounded at the apex, gradually narrowing to a subsessile base; flowers 1-2 in axils; pedicels 1.5-3.0 cm long; calyx ca 3 mm long, rather densely pubescent; corolla typically 1 cm or less wide; fruit 4-8 mm in diameter.

Southwestern United States and adjacent Mexico (Figure 11). Fairly widespread in this area, commonly occurring in disturbed soils along the roadside. Usually in association with *Prosopis* or *Larrea*. Principal flowering dates from March to June and August to October, depending on rains.

Chamaesaracha sordida is related to *C. pallida* and *C. coniodes*, probably more closely to the former. Further consideration of this species is found in the discussion of *C. coniodes*.

REPRESENTATIVE SPECIMENS: **Arizona:** COCHISE CO. 6 mi NW of Chiricahua, 18 May 1945, *Gould & Pultz* 3157 (ARIZ, GH, NY, UC, US). PIMA CO. 26 mi E of Tucson, 10 May 1935, *Maguire* 11214 (GH, NY). PINAL CO. 4 mi N of Christmas, *Anderson et al.* 1047 (ARIZ).

New Mexico: DE BACA CO. 7 mi W of Ft. Sumner, hwy 60, 15 Jun 1961, *Mahler* 1814 (OKLA). DONA ANA CO. Organ Mts, 15 Jul 1897, *Wooton* 156 (GH, NY, UC, US). EDDY CO. Carlsbad Caverns 24 May 1931, *Nelson* 11403 (GH, US). GRANT CO. 3 mi E of Red Rock, 20 May 1935, *Maguire et al.;* R 14. W., 12 Aug 1954, *Gordon & Buchanan* 74 (UNM). LEA CO. 5 mi NW of Hobbs, 7 Apr 1967, *Pearce* 2666 (ARIZ). LINCOLN CO. 5 mi W of Lincoln, 26 Jul 1938, *Hitchcock et al.* 4277 (UC). OTERO CO. Road to Rinconado, 15 Aug 1938, *Humphrey* 57 (ARIZ, UNM). SIERRA CO. Kingston, 10 Sep 1904, *Metcalfe* 1335 (GH, NY, UC, UNM, US). SOCORRO CO. 6.5 mi N of Old Bingham, and 2 mi E, 1 Aug 1949, *Dunn* 6067 (SMU).

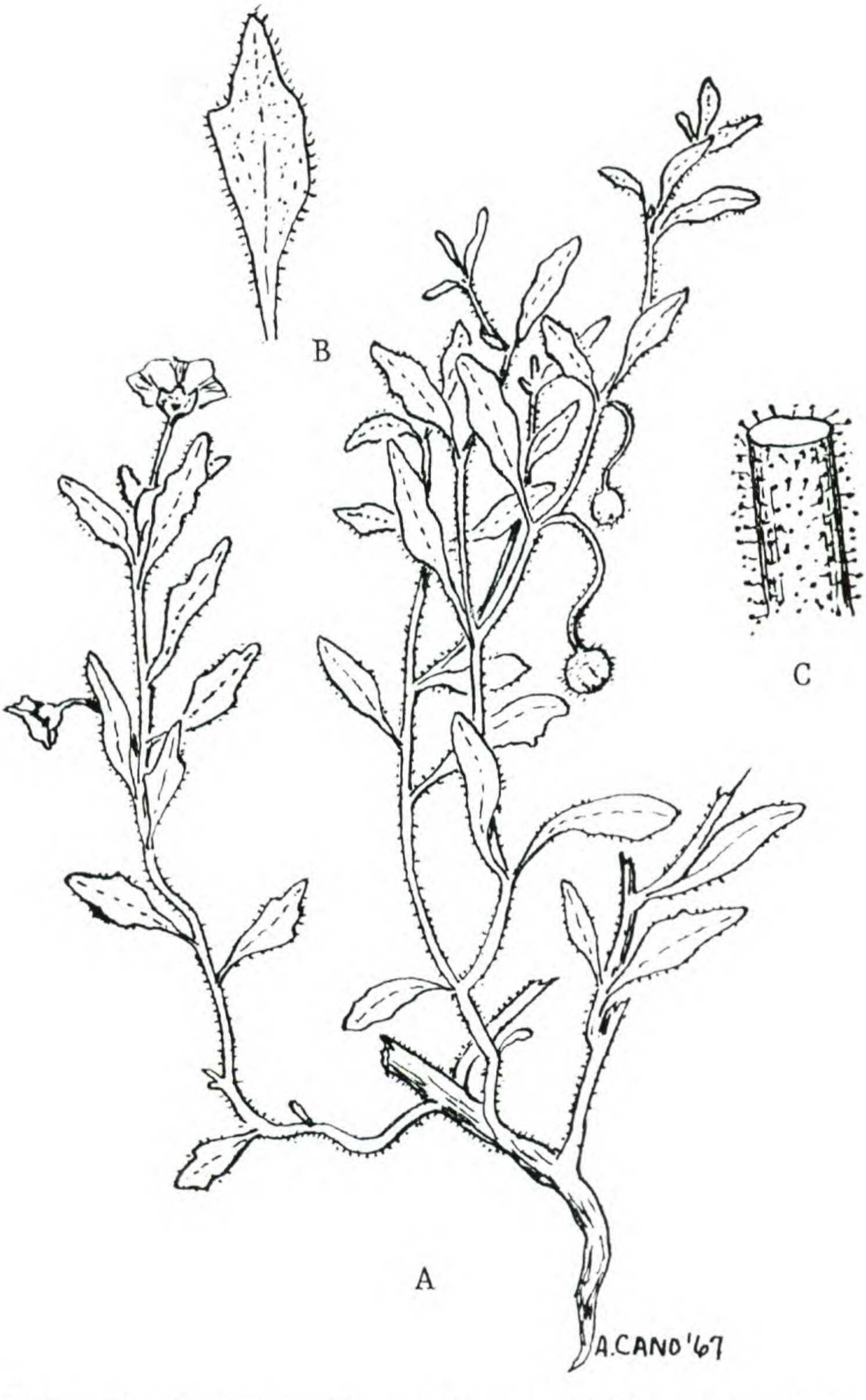

Figure 10. *Chamaesaracha sordida:* A, Habit sketch, × 1; B, Leaf, × 2; C, Stem, × 10.

Texas: BREWSTER CO. foothills of Chisos Mts, 19 Jun 1931, *Tharp s.n.* (GH, MICH, TEX, UC). BRISCOE CO. caprock W of Quitaque on Silverton road, 18 Jun 1945, *Whitehouse* 10001 (SMU). CRANE CO. 6 mi S of Crane, 11 Jul 1941, *Tharp s.n.* (GH, SMU). CROCKETT CO. roadside park over Pecos River Canyon, 26 Sep 1964, *Turner* 5109 (TEX). CULBERSON CO. below McKittrick Canyon, 23 Jul 1931, *Moore & Steyermark* (GH, MICH, NY, UC, US). DAWSON CO. 7 mi SE of Lamesa, 2 May 1967, *Shinners* 31814 (SMU). SIMMITT CO. 3 mi NW of Carrizo Springs, 2 May 1954, *Johnston et al.* 3543 (OKLA, TEX). EL PASO CO. El Paso, 16 Apr 1884 *Jones* 3704 (ARIZ, UC). FLOYD CO. 7 mi S of Floydad, 19 Jun 1964, *Delso* 57 (OKLA). GLASSCOCK CO. 10 mi W of Garden City, 26 Apr 1964, *Turner* 5015 (TEX). HOWARD CO. Scenic Mt, Big Spring, 14 Apr 1963, *Fields* 53 (OKLA). HUDSPETH CO. ca 30 mi E of El Paso, hwy 180, 7 Sep 1955, *Warnock* 13812 (TEX). LOVING CO. ca 10 mi E of Mentone, 3 Jun 1949, *Turner* 966 (SMU). LUBBOCK CO. Buffalo Springs, Lubbock, 29 May 1932, *Reed* 3494 (US). MAVERICK CO. Rio Grande River, Eagle Pass, 7 Mar 1852, *Schott s.n.* (NY). NOLAN CO. oilfield W of Sweetwater, 9 Jul 1941, *Tharp s.n.* (GH, TEX). PECOS CO. Ft. Stockton, 30 Jun 1938, *Warnock* T407 (ARIZ, GH, TEX, US). PRESIDIO CO. ca 20 mi SW of Marfa on Ruidoso road, 24 Jul 1966, *Averett* 153 (SMU, MO, TEX). RANDALL CO. floodplains, Red River, Palo Duro Canyon, 2 Sep 1907, *Ball* 1249 (NY, UC, US). REEVES CO. 25 mi N of Pecos, 4 Aug 1943, *Waterfall* 5491 (GH, NY). SCURRY CO. 12.6 mi E of Snyder, 16 Sep 1966, *Shinners* 31572 (SMU). STARR CO. 10 mi NW of Roma, 15 Mar 1964, *Pena* 21 (SMU). STONEWALL CO. 8.4 mi NW of Aspermont, 29 May 1963, *Shinners* 30036 (SMU). SUTTON CO. 10 mi W of Sonora, 30 Apr 1950, *Cory* 50054 (SMU). TAYLOR CO. ca 1 mi S of Wylie, 29 Mar 1963, *Henderson* 63-102 (SMU, TEX). TERRELL CO. 2-10 mi N of Sanderson, 1 Jun 1957, *Warnock & McBryde* 14868 (TEX). TOM GREEN CO. San Angelo, 18-19 May 1920, *Pennell* 10497 (NY). UPTON CO. 14 mi N of Rankin, 18 Apr 1933, *Cory* 5589 (GH). VAL VERDE CO. 5 mi NE of Juno, 7 Jun 1957, *Warnock & McBryde* 15078 (TEX). WEBB CO. 11 mi S of Laredo, 23 Mar 1963, *Robles* 16 (SMU). WINKLER CO. 10 mi N of Kermit, 8 Dec 1965, *Collins* 1088 (SMU). ZAPATA CO. 22 mi S of Laredo, 4 Apr 1965, *Guerra et al.* 609 (ARIZ, TEX).

Mexico: CHIHUAHUA, 3.5 mi S of Trincheras, 10-12 Aug 1941, *Johnston* 8061 (GH). COAHUILA, Muzquiz, Apr 1938, *Marsh* 1179 (OKLA, SMU, TEX). NUEVO LEON, 23 mi N of Sabinas Hidalgo, 26 Mar 1944, *Webster & Barkley* 14580 (NY, TEX, UC).

7. **Chamaesaracha coniodes** (Moric. ex Dunal) Britt., Mem. Torr. Bot. Club 5: 287. 1895. Lectotype (G) not seen: MEXICO: Canada Verde, between Lardo and Bexar [San Antonio], [TEXAS: McMullen Co] Mar 1828.

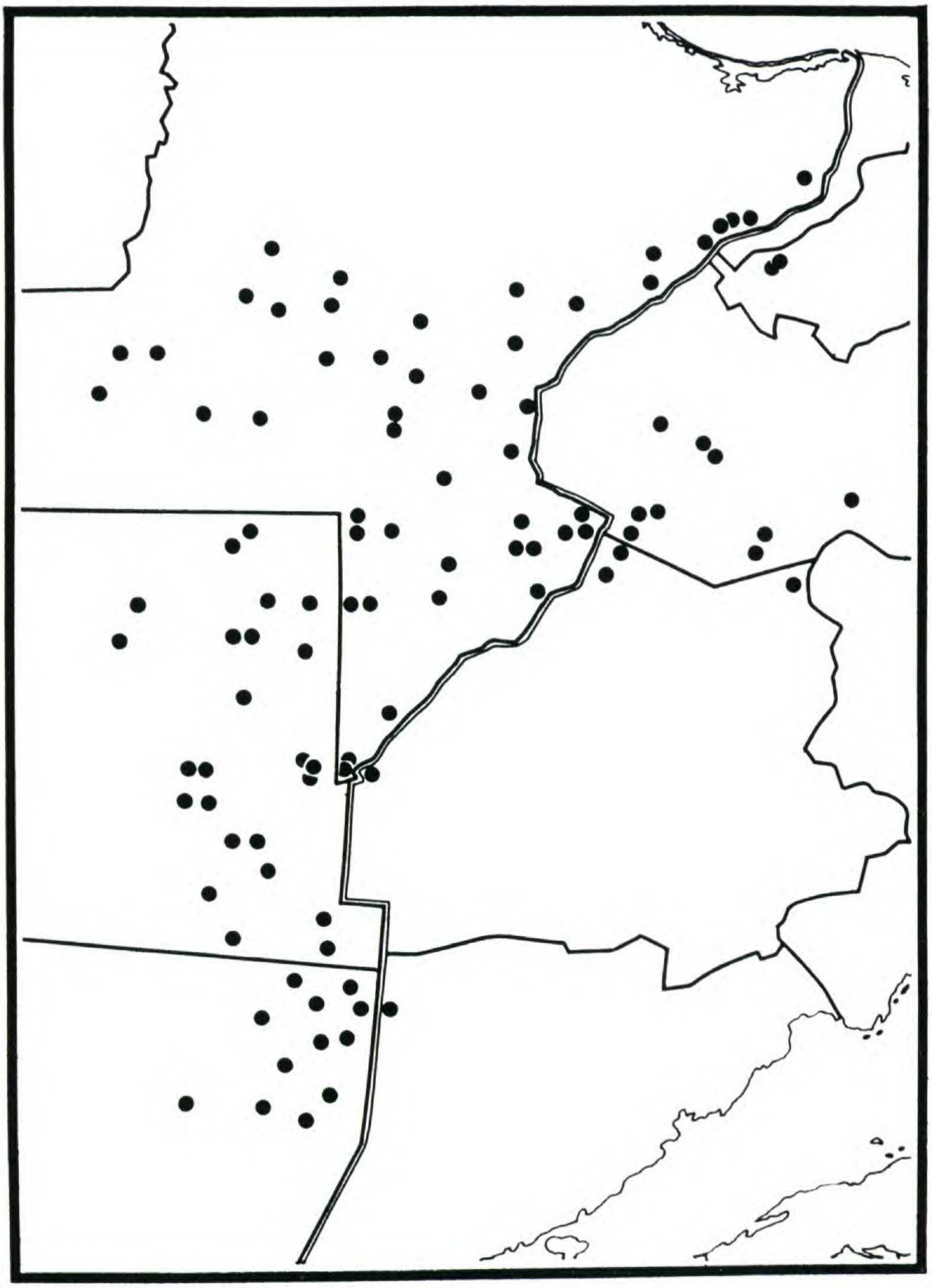

Figure 11. Distribution of *Chamaesaracha sordida*.

Berlandier 1494 (=234). Isotype GH! *Berlandier* 1463 (=203) was also cited in the original description, but I have selected the other collection since the specimen at GH is the only one I have seen. Fig. 12.
Solanum coniodes Moric. ex Dunal, in D.C. Prod. 13(1): 456. 1852.

Rhizomes subligneous to woody; stems prostrate or ascending, 9-30 cm long, 2.0-3.0 mm in diameter, pubescent; herbage pubescent with simple trichomes, occasionally mixed with fewer glandular hairs, usually somewhat villous; leaves broadly lanceolate, 2.5-5.5 cm long, 1.0-2.0 cm wide, crenate to deeply and pinnately lobed; apex acute to rounded, base attenuate, subsessile; flowers 1-2 in axils; pedicel 2.0-3.5 cm long; calyx ca 4.0 mm high; corolla 1.0-1.5 cm wide; fruit ca 7 mm in diameter, chromosome number, $n = 24, 36$.

Southwestern United States and adjacent Mexico (Figure 13). Fairly widespread, commonly occurring in disturbed soils along the roadside, usually in association with *Prosopis* or *Larrea*. Principal flowering dates, March to June and August to October, depending on rains.

Chamaesaracha coniodes was merged with *C. sordida* by Gray (1876). However, the two species may be distinguished by the characters given in the key to the species. Chemical and chromosomal differences also serve to distinguish the two species. In areas of sympatry both taxa retain their diagnostic features, even in mixed populations and, hence, appear to be good biological species.

REPRESENTATIVE SPECIES: **Colorado:** BACA CO. breaks of Carrizo Creek, 5 mi SW of Kirkwell, 29 Aug 1949, *Weber* 5120 (SMU, UC). LAS ANIMAS CO. Tecolate mesa, near Troy, 15 Jul 1947, *Rogers* 4848 (MICH, UC).

Kansas: CLARK CO. 9 mi N of Ashland, 28 Apr 1939, *Horr* E249 (OKLA, SMU, TEX, UC, US). ELLIS CO. Smoky Hill River, 22 Jun 1935, *Bondy* 121 (ARIZ, OKLA, US). FINLEY CO. 4 mi W of Kalvesta, 2 Jun 1967, *Stephens* 11300 (OKLA, SMU, UC). HAMILTON CO. Syracuse, 5 Jul 1893, (OKLA, SMU, UC); Syracuse, 5 Jul 1893, *Thompson* 190 (NY, UC). MORTON CO. 9 mi N, 3 mi W of Elkhart, 7 Jun 1961,

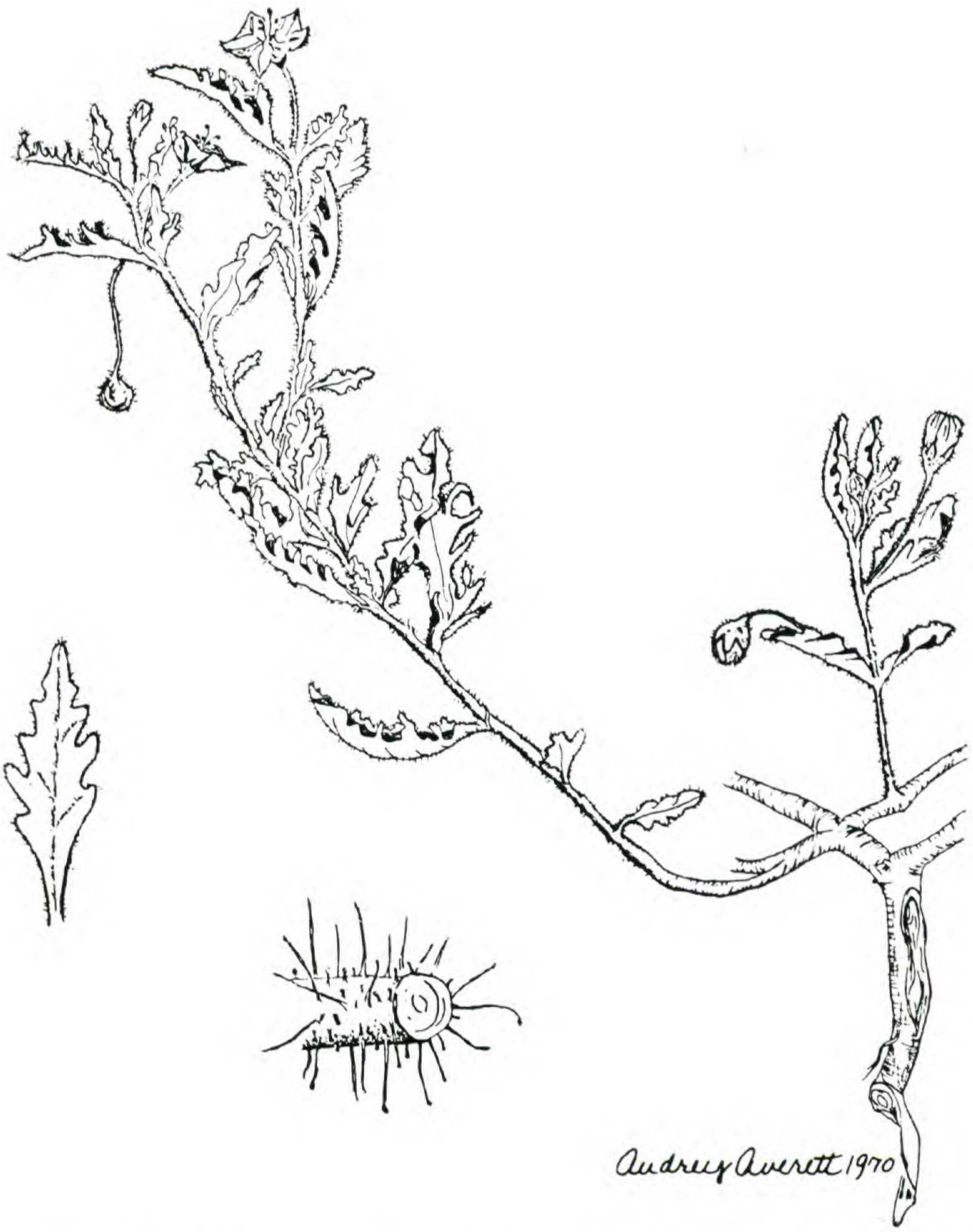

Figure 12. *Chamaesaracha coniodes:* A, Habit sketch, × 1; B, Stem, × 15; C, Leaf, × ca. 1.

Richards 2559 (SMU). SEWARD CO. 12 mi N of Liberal, 8 Jul 1960, *McGregor* 15778 (SMU). ULYSSES GRANT CO. cellar excavations, 26 Jun 1893, *Thompson* 29 (GH, NY, UC, US).

New Mexico: CURRY CO. 5.7 mi W of Melrose, 5 Aug 1945, *Shinners* 20905 (SMU). DE BACA CO. 2 mi N of Ft. Sumner, 3 Jun 1969, *Tomb* 497 (TEX). LINCOLN CO. Gray, 6 Jun 1898, *Skehan* 37 (GH, NY, US). QUAY CO. S of San Juan, 26 Aug 1945, *Waterfall* 6123 (GH, NY, OKLA, SMU). SAN MIGUEL CO. 5 mi SW of Las Vegas, 11 Aug 1949, *Gordon & Norris* 495 (UNM). SIERRA CO. Elephant Butte Dam, 30 Apr 1933, *Nelson s.n.* (UNM). UNION CO. 3 mi W of Oklahoma line W of Kenton, 11 Jun 1948, *Rogers* 5960 (MICH, US).

Oklahoma: BEAVER CO. 2 mi W of Turpin, 16 Aug 1960, *Hindman* 236 (OKLA). BECKHAM CO. 2 mi E of Sayne, 9 Aug 1927, *Stratton* 354 (SMU). CIMARRON CO. 3.5 mi N of Kenton, 7 Oct 1950, *Waterfall* 9714 (ARIZ, OKLA, SMU). CUSTER CO. 1 mi W, 1 mi S of Weatherford, 11 May 1952, *Waterfall* 10716 (OKLA, SMU). ELLIS CO. 3.8 mi S of Shattuck, 25 Sep 1964, *Shinners* 30415 (SMU). GREER CO. near Granite, *Stevens* 1010 (GH, OKLA, US). HARMON CO. floodplain of Elm Fork, 14 mi S of Erick, 25 May 1940, *Waterfall* 2002 (GH, NY, OKLA). JACKSON CO. 6 mi SE of Duke, 29 May 1957, *Waterfall* 13105 (ARIZ, OKLA, US). KIOWA CO. 1.7 mi N of Snyder, 23 Apr 1938, *Fry* 186 (OKLA). MAJOR CO. near Waynoka, 23 May 1913, *Stevens* 599 (GH, NY, OKLA). OKFUSKEE CO. 2 mi E of Paden, 7 Jun 1938, *Ray* 94 (OKLA). SWANSON CO. near Mountain Peak, 23 Jun 1913, *Stevens* 1239 (GH, OKLA). TILLMAN CO. 2 mi S of Frederick, 2 Apr 1961, *Myrick* 49 (OKLA). WOODS CO. 8 mi NW of Alva, 8 May 1932, *Stratton* 3014 (OKLA).

Texas: BAILEY CO. Muleshoe Nat'l Wildlife Refuge, 20 mi S of Muleshoe, 18 Jun 1964, *Rosson* 576 (OKLA, UC). BAYLOR CO. 4.2 mi ENE of Mabelle, 24 Apr 1954, *Shinners* 18584 (SMU). BELL CO. near Sparta, 4 May 1931, *Wolff* 2885 (US). BORDEN CO. red bed lands Colorado to Gail, 25 May 1899, *Bray s.n.* (TEX). BREWSTER CO. hwy 90 12 mi E of Alpine, 8 Sep 1966, *Averett & Watson* 161 (SMU, MO, TEX). BROWN CO. Brownwood, 31 Mar 1917, *Palmer* 11439 (UC). CALLAHAN CO. hwy 183, 4.2 mi S of Baird, 29 Sep 1950, *Cory* 58391 (SMU). CASTRO CO. Nazareth Community, 3 May 1946, *Rachaner* 32 (TEX). CHILDRESS CO. Childress, 21 Apr 1968, *Shinners* 32179 (SMU). COLEMAN CO. 1 mi SE of Santa Anna, 9 Jun 1957, *Shinners* 26386 (SMU). COTTLE CO. S Pease River, 12 mi NE of Paducah, 29 Apr 1963, *Rowell* 8072 (OKLA). COMAL CO. Comanche Springs New Braunfels, etc., Jun 1851, *Lindheimer* 1037 (GH, NY, SMU, TEX, UC, US). COMANCHE CO. 8 mi N of Comanche, 6 Apr 1968, *Seale* 32 (OKLA). DALLAM CO. Rita Blanca Creek, N of Dalhart, Aug 1949, *York & Rodgers* 252 (OKLA, SMU, TEX). DICKENS CO. 2 mi N of Dickens, 28 Jun 1964, *Rowell* 10301 (OKLA). DIMMIT CO. Carrizo Springs, 30 Apr 1930, *Hoaglund s.n.* (TEX). DUVAL CO. 6 mi W of Freer, 20 Mar

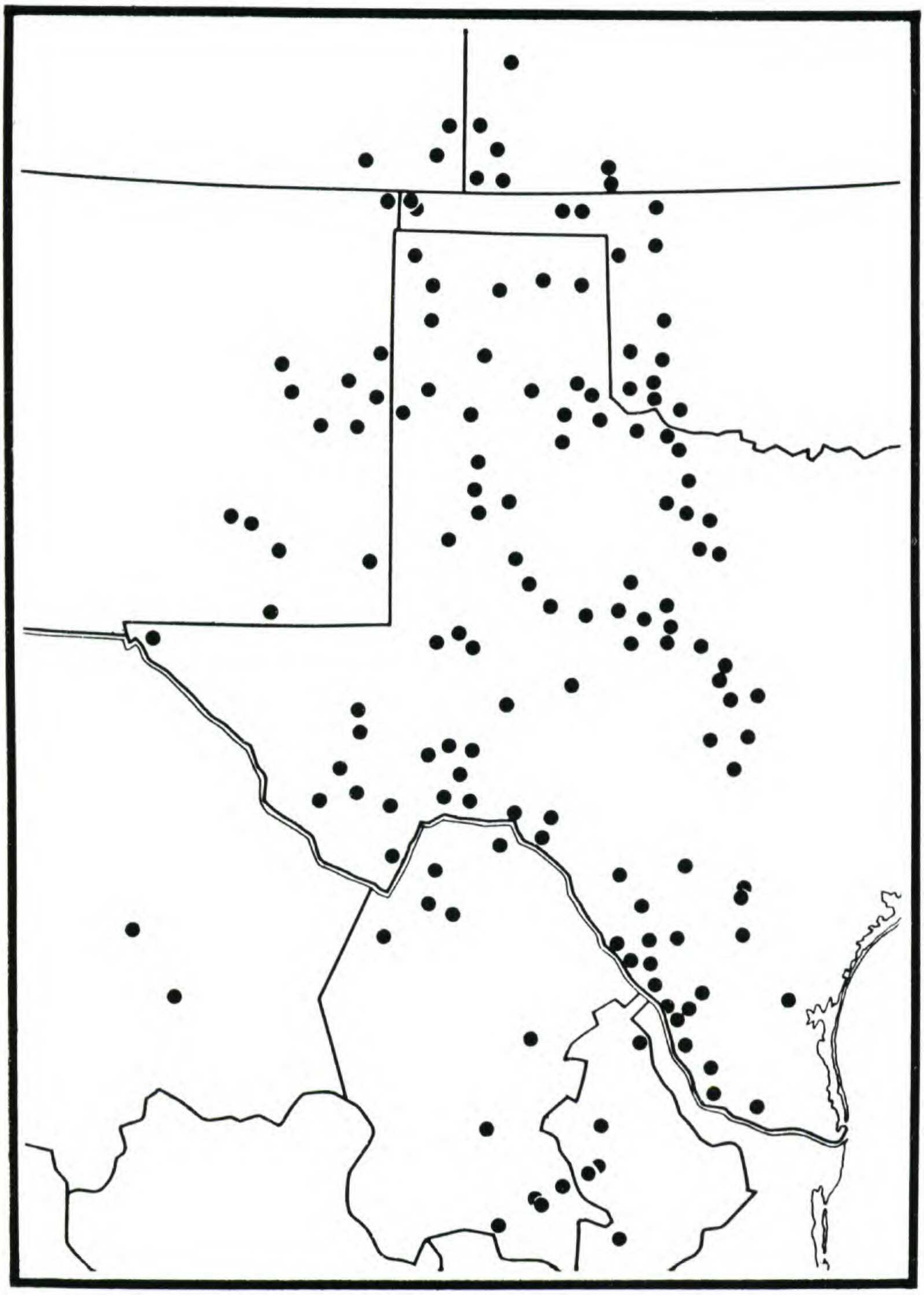

Figure 13. Distribution of *Chamaesaracha coniodes*.

1960, *McCart* 7188 (OKLA). EASTLAND CO. Rising Star, 11 Dec 1931, *Potter s.n.* (TEX). ECTOR CO. NE Odessa, 28 Mar 1967, *Averett* 227 (SMU, MO, TEX). EDWARDS CO. 28 mi W of Rockspring, 18 Apr 1929, *Cory* 689 (GH). EL PASO CO. Loyal Valley (Frontera), 22 May 1852, *Buckley* 7837 (SMU). ERIO CO. hwy 81, 6 mi N of Dilley, 21 Mar 1964, *Vasquez* 50 (SMU, TEX). GARZA CO. Post, 4 Jun 1925, *Ruth* 1270 (MICH, US). HALE CO. 4 mi N of Hale Center, 17 Jul 1968, *Averett & Tomb* 354 (SMU, MO, TEX). HALL CO. *ca* 4 mi from hwy 287, E of Estelline, 6 Sep 1945, *Whitehouse* 10736 (MICH, SMU, US). HAMILTON CO. 5 mi ESE of Hamilton, 14 Apr 1965, *Shinners* 30952 (SMU). HARDEMAN CO. 2 mi W of Quanah, 5 May 1963, *Stokes* 65 (OKLA). HARTLEY CO. junct. of hwy 87 & 385 near Hartley, 16 Jul 1968, *Averett & Tomb* 351 (SMU, MO, TEX). HEMPHILL CO. 7 mi NE of Canadian, 20 Jun 1964, *Brown* 76 (OKLA). HIDALGO CO. 2 mi S of Alamo, 7 Dec 1933, *Clover* 1482 (MICH, NY). HOCKLEY CO. 10 mi E of Levelland, 20 Apr 1964, *Forhand s.n.* (OKLA). HUTCHINSON CO. Canadian River breaks, 4 May 1965, *Drake* 45 (TEX). JACK CO. 3 mi W of Jacksboro, 14 Apr 1946, *Whitehouse* 15308 (SMU). JEFF DAVIS CO. hwy 166, 1 mi S of Ft Davis, 26 Jun 1966, *Averett* 136 (SMU, MO, TEX). JIM HOGG CO. 5 mi E of Hebbronville, 16 Mar 1963, *Areola et al.* 119 (SMU, TEX). LIVE OAK CO. hwy 59, 15 mi SW of George West, 13 Mar 1965, *Rodriquez* 17 (ARIZ, TEX). LUBBOCK CO. ca 5 mi N of Slayton, 17 Jul 1968, *Averett & Tomb* 356 (SMU, MO, TEX). LYNN CO. 11 mi W of Tahoka, 25 Apr 1954, *Shinners* 18621 (SMU). MAVERICK CO. 30 mi SE of Eagle Pass, 14 Mar 1964, *Bruni* 13 (OKLA, SMU, TEX). MC MULLEN CO. 15 mi N of Freer, 28 Apr 1958, *Thompson & Graham* 80 (TEX). MIDLAND CO. 15.6 mi ESE of Midland, 30 May 1963, *Shinners* 30101 (SMU). MILLS CO. 2 mi N of Priddy, 26 Sep 1950, *Cory* 58175 (OKLA, SMU). MOTLEY CO. 3.3 mi W of Matador, 28 Apr 1954, *Shinners* 18693 (SMU). NOLAN CO. Sweetwater, 27 May 1918, *Palmer* 13709 (US). OCHILTREE CO. Canadian River, 27 mi S of Perryton, 19 Sep 1958, *Wallis* 7820 (SMU, TEX). OLDHAM CO. Tascosa, 16 Jun 1932, *Reed* 3515 (US). RANDALL CO. entrance to Palo Duro State Park, 17 Jul 1968, *Averett & Tomb* 353 (SMU, MO, TEX). REEVES CO. S of Pecos, 31 Mar 1942, *Nelson & Nelson* 5004 (GH). ROBERTS CO. Canadian River Valley, 27.5 mi S of Perryton, 6 Jun 1958, *Wallis* 7172 (OKLA, TEX). PALO PINTO CO. 9 mi ENE of Gordon, 6 May 1951, *Shinners* 13230 (SMU). PARKER CO. 16.5 mi SW of Weatherford, Brazos River bottoms, 4 Apr 1948, *Shinners* 9971 (SMU). PECOS CO. 1 mi E of Ft Stockton, 19 Apr 1946, *Warnock* 46151 (TEX, UC). PRESIDIO CO. Spur Ranch, S of Marfa, 10 Aug 1941, *Warnock* 21370 (TEX). SAN PATRICIO CO. near Mathis, 5 Apr 1931, MC KELVEY 1724 (GH, US). SAN SABA CO. 20 mi W of Cherokee, 4 Apr 1966, *Henderson* 8 (TEX). SHACKELFORD CO. ½ mi N of Callahan Co line on hwy 283, 24 Apr 1963, *Henderson* 63-516 (SMU, TEX). STARR CO. 9 mi N of Roma, 13 Apr 1962, *Alvarez et al.* 8043 (TEX).

TAYLOR CO. Camp Barkeley, 25 Oct 1942, *Tolstead* 5779 (NY, SMU). TERRELL CO. 1 mi E of Sanderson, 30 Apr 1949, *Warnock & Turner*, 599 (SMU). TERRY CO. 5 mi E of Brownfield, 25 Apr 1954, *Shinners* 18618 (SMU). THROCKMORTON CO. 8.3 mi E of Throckmorton, 29 Apr 1954, *Shinners* 18806 (SMU). TOM GREEN CO. San Angelo, 3 Jul 1917, *Palmer* 12379 (UC). TRAVIS CO. Onion Creek, near Austin, 17 May 1918, *Young s.n.* (TEX). UVALDE CO. Garner State Park, 5 Apr 1969, *Tomb* 391 (TEX). VAL VERDE CO. E city limits, Del Rio, 5 Apr 1969, *Tomb* 401 (TEX). WEBB CO. Laredo, 15 Mar 1917, *Palmer* 11286 (UC). WICHITA CO. Red River 7.4 mi N of Electra, 30 Mar 1945, *Whitehouse* 9590 (MICH, SMU, US). YOUNG CO. 3 mi W of New Castle, 2 Apr 1938, *McCart* 873 (SMU). ZAPATA CO. 1.5 mi S of San Ygnacio, 31 Jan 1954, *Shinners* 17690 (SMU). ZAVALA CO. near Batesville, 25 Mar 1961, *Stewart* 58 (OKLA).

Mexico: CHIHUAHUA, Mts NW of Chihuahua, 1 Aug 1936, *Le Sueur* 47 (OKLA, TEX UC). COAHUILA, 24 mi W of Cd Acuna, 20 Aug 1966, *Powell et al.* 1412 (SRSC, TEX). NUEVO LEON, 12 mi E of Monterrey, 27 Feb 1944, *Barkley* 14351 (GH, TEX, UC).

EXCLUDED SPECIES

C. potosina Rob. & Greenm.
= **Saracha potosina** (Rob. & Greenm.) Averett
C. boliviensis Dammer
= **Solanum chamaesarachidium** (Dammer) Bitt.
C. grandiflora (Hook.) Fernald
= **Leucophysalis grandiflora** (Hook). Rydb.
C. nana Gray
= **Leucophysalis nana** (Gray) Averett
C. heterophylla Hemsl.
= **Leucophysalis heterophylla** (Hemsl.) Averett
C. japonica Fr. & Sav.
= **Physaliastrum japonicum** (Fr. & Sav.) Honda
C. echinata Yatabe
= **Physaliastrum japonicum** (Fr. & Sav.) Honda
C. savatieri Makino
= **Physaliastrum savatieri** (Makino) Makino
C. watanabei Yatabe
= **Physaliastrum savatieri** (Makino) Makino
C. sinensis Hemsl.
= **Physalis sinensis** (Hemsl.) Averett
C. physaloides Green
= **Physalis labata** Torr. fide Waterfall (1958).

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